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A publication of THE SOCIETY OF ECONOMIC PALEONTOLOGISTS AND MINERALOGISTS *and* THE PALEONTOLOGICAL SOCIETY *with the generous support and cooperation of* THE AMERICAN ASSOCIATION OF PETROLEUM GEOLOGISTS *and* THE GEOLOGICAL SOCIETY OF AMERICA

VOLUME 28 SEPTEMBER, 1954 NUMBER 5

STROPHALOSIA IN THE PERMIAN OF QUEENSLAND

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ABSTRACT—Ten species and varieties of *Strophalosia* King occur in the Permian faunas of Queensland. Their wide geographical distribution and restricted stratigraphical range have made possible the correlation of marine formations throughout Queensland. The taxonomy of the genus is extremely complex, and present evidence indicates that *S. gerardi* King, although the only species eligible under the International Rules of Zoological Nomenclature, is most unsuited for selection as the type species. Reasons for the suspension of the Rules to permit the designation of *S. goldfussi* Muenster as the type species are given. The subgenera *Branxtonia* Booker and *Wyndhamia* Booker are placed in the synonymy of *Strophalosia*. Of the Queensland species, all except *S. jukesi* var. *concava* belong to the "*preovalis-clarkei-ovalis*" plexus which evolved during Sakmarian, Artinskian and Kungurian times. Variations within each species appear to be closely related to the process of articulation, and this relation of form and function is discussed. Species and varieties described as new are: *Strophalosia preovalis*, *S. p.* var. *pristina*, *S. p.* var. *warwicki*, *S. brittoni*, *S. b.* var. *gattoni*, *S. clarkei* var. *minima*, *S. ovalis*, and *S. jukesi* var. *concava*.

STRATIGRAPHICAL INTRODUCTION

Permian marine formations in Queensland.—Sedimentation during Permian times was restricted to the eastern mobile belt, the Tasman Geosyncline, the tectonics of which have been summarised by Hill (1951). Four main basins, trending north-northwest and separated by high ridges of older Paleozoic rocks, received the sediments. These basins originated at various stages during upper Paleozoic times and their subsequent histories differed in many respects. Today, the main exposures are found in the following regions:

1. Bowen Basin. The earliest marine sediments are of Permian age. Fossiliferous strata occur along the northern and eastern margins of the basin in the Collinsville-Mt. Britton-Nebo and Dawson River districts, and on the Springsure shelf in the west. This basin is bordered by the Anakie anticline and the Bogie-Gogango high (Hill, 1951).

2. Yarrol basin. Marine sedimentation began in late Middle Devonian times and continued into early Permian. The basin was formed to the west of the Gogango high, and extends from Mackay south through Rockhampton and Mundubbera. The exposure of Permian sediments in the Texas district is believed to represent a southern continuation of the basin.

3. Esk basin. Permian marine sediments occur at the base of the sequence in this basin which was formed by rifting in the South Coast high. The fault blocks of the Silverwood area may represent remnants of the basin. Fossiliferous strata are exposed at Cressbrook and Northbrook near Est.

4. Maryborough basin. This is situated

to the east of the South Coast high, and first received sediments in early Permian times. Fossiliferous strata are exposed in the Gympie-Gigoomgan district.

The Permian sequence in the Springsure district has been studied in greatest detail, and it has been used as a basis for stratigraphical correlations throughout Queensland. It was investigated by Jensen (1926), Reid (1930), Reeves (1947) and Hill (1952, pp. 41–43), and the following succession has been recognised to the east of the Anakie anticline.

	Feet
Bandanna beds	1600
Mantuan Downs *Productus* bed	50
Catherine beds	400– 700
Ingelara beds	90– 500
Aldebaran sandstone	1600–2500
Cattle Creek beds	500
Staircase sandstone	up to 1600
Dilly beds	exposed 2000

The Dilly, Cattle Creek, Ingelara and Mantuan Downs *Productus* formations contain marine faunas. Fossils have not been found in the other beds. This sequence was formed on the western margin of the Bowen basin and differs from that found in the north and east. West of the Anakie anticline the Mantuan Downs *Productus* bed is the only fossiliferous marine formation in the succession.

Reid (1929) investigated the stratigraphy of the Collinsville-Nebo district and found at least three horizons containing different species of *Strophalosia* in the Middle Bowen beds. Apparently there is a facies change towards the south, as the Collinsville coal measures are replaced by fossiliferous marine sediments in the Blenheim-Mt. Britton-Nebo belt. The sequence may be summarised as follows:

	Feet
Upper Bowen beds	
Non-marine	9600
Middle Bowen beds	
Middle Bowen marine beds	2400
Collinsville coal measures (Mt. Britton beds)	700
Lower Bowen volcanics	5400

In the Middle Bowen marine beds, the main formation is the Big *Strophalosia* bed, the basal part of which is best exposed at Gattonvale, the upper part being best exposed in Parrot Creek. This formation which varies considerably in thickness, extends around the nose of the Bowen basin at Collinsville and as far south as Mt. Britton. Near Cracow in the southeastern part of the basin, three fossiliferous horizons have been found. The early Artinskian fauna (Hill, 1950) occurs $\frac{1}{4}$ to $\frac{1}{2}$ mile west of the Cracow Homestead, while a younger fauna, equivalent to that of the Ingelara beds and the lower part of the Big *Strophalosia* bed, is found on the Cracow-Theodore road, between Oxtrack and Delusion Creeks. A third fauna, equivalent to the upper part of the Big *Strophalosia* bed, occurs at Fossil Hill, 2.2 miles west of Cracow township. Further field investigations are necessary before the succession in the Cracow district can be determined satisfactorily.

In the Yarrol basin the sequence has not been studied in detail, although the earliest Permian fauna is equivalent to the Artinskian fauna of Cracow, and those of the Cattle Creek and Mt. Britton beds. The Ingelara and Mantuan Downs faunas are not represented in the Yarrol basin, as non-marine conditions developed early in Permian times. The Artinskian fauna at Texas has not yielded any specimens of *Strophalosia*.

In the Esk basin, the Ingelara fauna has been found in the Cressbrook fault block (Campbell, 1953a), and the author has found representatives of the Cattle Creek fauna at Oaky Creek in the same fault block. The Silverwood fault blocks were investigated by Richards and Bryan (1924) and their interpretation of the succession was later modified by Bryan and Jones (1946, p. 45). Four horizons containing four different species of *Strophalosia* occur in these fault blocks, and three of the species are found in the Springsure and Collinsville districts.

Strophalosia has not been found in the Permian faunas of the Maryborough basin.

Correlation of fossiliferous horizons in Queensland.—The correlations given in the following table are based on the distribution of *Strophalosia*. In the Bowen basin three main faunas are found, and at Dilly in the Springsure district a fourth occurs in the earliest beds. The position of the fauna which occurs in the Wallaby Rocks beds of the Silverwood district, has not been determined and this fauna is not represented

TABLE 1

Springsure District	Bowen-Nebo District	Cracow	Yarrol	Fault-Blocks	
				Silverwood	Cressbrook
Bandanna beds	Upper Bowen beds				
Mantuan *Productus* bed	(upper part)	Fossil Hill bed		Condamine Bl. upper bed	
Catherine sandstone	Big *Strophalosia* Bed				
Ingelara beds	Middle Bowen (lower Gattonvale bed)	Oxtrack Ck. bed		Condamine Bl. lower bed	Upper horizon
Aldebaran sandstone	Collinsville coal measures				
Cattle Ck. beds	Nebo-Mt. Britton-Blenheim beds	Cracow homestead	*Springsurensis* bed	Stanthorpe Rd. Bl. *Eurydesma* bed	Lower bed (Oakey Ck.)
Staircase sandstone	Lower Bowen volcanics				
Dilly beds					

on the table. The geographical distribution of the species is illustrated on Map I.

Correlations with faunas in other states.—New South Wales.—At Kimbriki, *S. preovalis* var. *warwicki* has been found in beds which have been equated with the lower Marine series. This species is characteristic of the *Eurydesma* beds which are equivalent to the Cattle Creek beds. *S. typica* and *S. clarkei*, both characteristic of the Ingelara beds in Queensland, have been found in the Branxton stage of the upper Marine series near Branxton and Nowra respectively.

Tasmania.—*S. jukesi* from the Cascades stage, has no representatives in Queensland, but its associated fauna is similar to the Artinskian fauna of Cracow.

West Australia.—Species of *Strophalosia* have been found in the following beds—Callytharra, Fossil Cliff, Wandagee, Nooncoonbah and the upper Ferruginous beds—all of which have been equated by Teichert (1941, p. 399) with the Artinskian. The species figured as *S. jukesi* by Prendergast (1943, pl. 5, figs. 18–20) resembles *S. typica* Booker, but the other species show little similarity to their eastern contemporaries.

Ages of the Queensland faunas.—*Strophalosia* is not abundant in the Permian of Timor, Broili (1916) recording only the one species, *S. indica*, from the Basleo beds. This species which also occurs in the upper *Productus* limestone of the Salt Range (Waagen 1884, pp. 648–655), resembles *S. clarkei* (Ingelara and early Mantuan Downs faunas) in its external proportions, but other characters are dissimilar. *S. sublamellata* Reed (1944, pp. 107–108), from the lower *Productus* limestone, is somewhat similar to *S. preovalis* (Cattle Creek beds). Gerth (1950, p. 312, table 7) correlated the Basleo beds with the upper part of the middle *Productus* limestone, determining their age as Kazanian. Teichert (1941) equated them with the early part of the limestone which he determined as Kungurian. Similarity of faunas of the Ingelara and Branxton beds in eastern Australia suggests equivalence of age, the latter having been correlated by Teichert and Fletcher (1943) with the Artinskian-Kungurian of Russia. Campbell (1953b), in his investigation of the Ingelara fauna reached the same conclusion. The age of the early Cracow fauna, which is equivalent to that of the Cattle Creek beds, was determined by Hill (1950) as Sakmarian or early Artinskian. Thus the approximate ages of the various faunas are as follows:

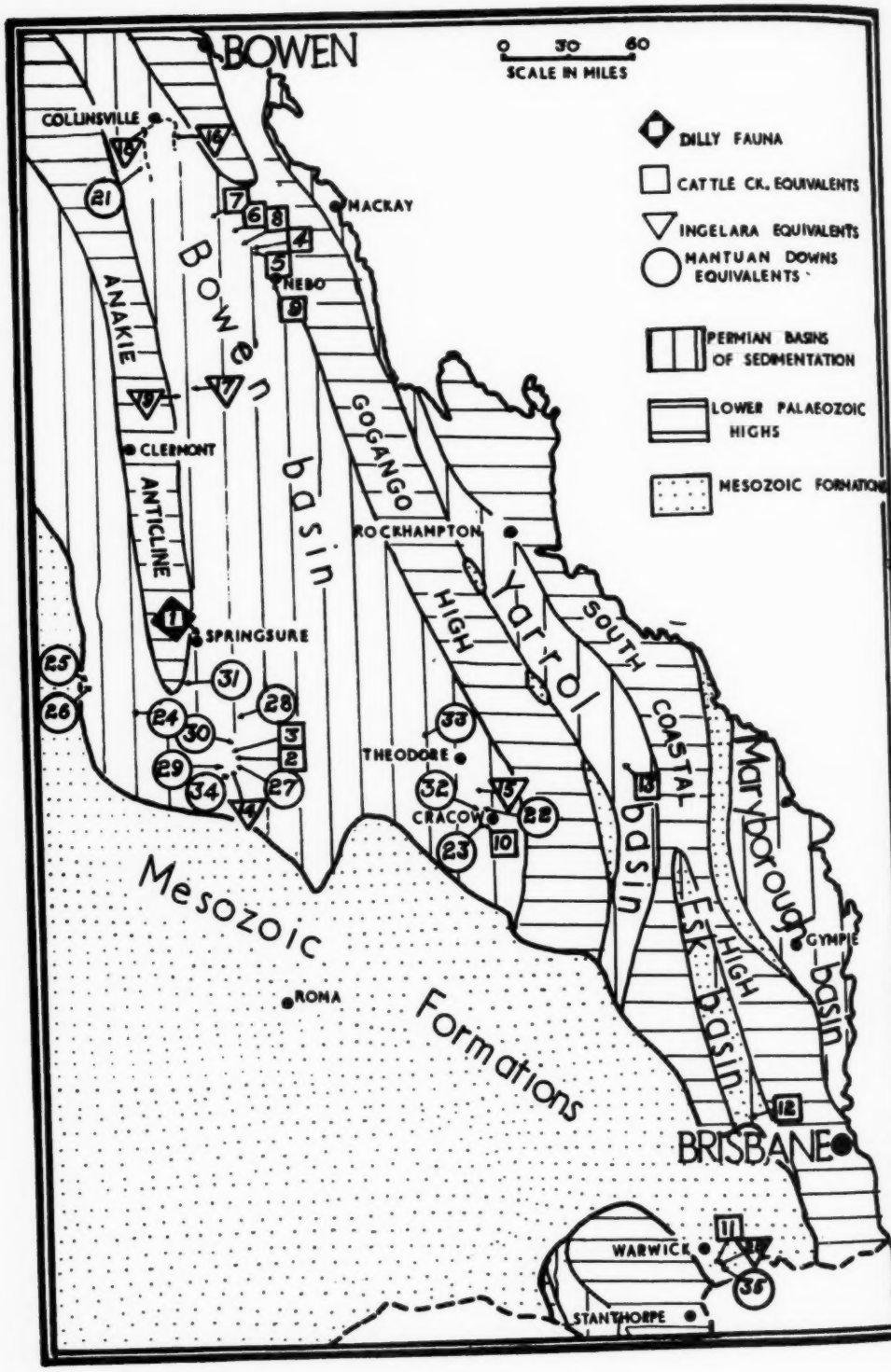
BOWEN
0 30 60
SCALE IN MILES
COLLINSVILLE
MACKAY
NEBO
CLERMONT
SPRINGSURE
ROCKHAMPTON
THEODORE
CRACOW
WARWICK
STANTHORPE
BRISBANE
GYMPIE
RONA
ANAKIE
ANTICLINE
Bowen basin
GOGANGO HIGH
Yarrol
SOUTH COASTAL basin
Maryborough basin
ESK HIGH
ESK basin
Mesozoic Formations
DILLY FAUNA
CATTLE CK. EQUIVALENTS
INGELARA EQUIVALENTS
MANTUAN DOWNS EQUIVALENTS
PERMIAN BASINS OF SEDIMENTATION
LOWER PALAEOZOIC HIGHS
MESOZOIC FORMATIONS

TABLE 2

Age	Springsure District	Collinsville District
Kungurian	Mantuan Downs *Productus* bed	(upper part, Parrot Creek)
		Big *Strophalosia* bed (lower part, Gattonvale)
	Ingelara beds	
Artinskian		
Sakmarian	Cattle creek beds	Mt. Britton beds
	Dilly beds	Lower Bowen volcanics

SYSTEMATIC PALEONTOLOGY

The terminology used in the following descriptions has been defined by Muir Wood (1928) and Prendergast (1943). Stainbrook's classification (1947) has been adopted, with slight modifications.

FIG. *1*—Map of Localities.

Dilly beds (*S. preovalis* var. *pristina*)

1. Two miles north of the Dilly railway station, Springsure district.

Cattle Creek beds and their equivalents. (*S. preovalis* s.s., *S. preovalis* var. *warwicki*, *S. brittoni*).

2. Middle Consuelo Creek, Serocold district.
3. Cattle Creek, 2 miles upstream from its junction with Consuelo Creek.
4. Mt. Britton, 3 miles southwest of township.
5. Dullawanna station, Mt. Britton district.
6. Eungella station, 4 miles southwest.
7. Blenheim.
8. Homevale.
9. Perry's Paddock, Nebo district.
10. Cracow homestead, ¼–½ mile west.
11. *Eurydesma* Beds, Stanthorpe Road fault block.
12. Oaky Creek region, Cressbrook—Buaraba district.
13. Yarrol homestead, Burnett valley.

Ingelara beds and their equivalents. (*S. clarkei*, *S. typica*, *S. brittoni* var. *gattoni*, *S. jukesi* var. *concava*).

14. One-half mile north of the road in Dry Creek, Ingelara station.
15. Erosion gully on the Cracow-Theodore road, between Delusion and Oxtrack Creeks.
16. Gattonvale Outstation, Collinsville district.
17. Clermont-Nebo telegraph line, 84 chains north of the Denham Range.
18. Collinsville district (see Reid, 1929).
19. Logan Downs, Clermont district.
20. Marine horizon in the Wallaby Rocks, immediately above the plant beds, Stanthorpe Road fault block.

Mantuan Downs *Productus* bed and its equivalents. (*S. ovalis*, *S. clarkei* var. *minima*).

21. Parrot Creek, 4½ miles upstream, Collinsville district.
22. Fossil Hill, 2.2 miles west of the Cracow township.
23. Cracow station, 1.3 miles northwest of the homestead.
24. Nardoo, west of Springsure.
25. Fairview homestead, west of Springsure.
26. 2 miles east of Mantuan Downs homestead, west of Springsure.
27. Sandy Creek, Rewan station, south of Springsure.
28. Peawaddy Creek, southwest of Rolleston, Springsure district.
29. Consuelo Creek, above Black Alley, Upper Consuelo holding.
30. South Consuelo Creek, east flank of Serocold anticline.
31. Three miles west of Wealwandangie Head station, west of Springsure.
32. Cracow-Theodore road, 3 miles from Cracow.
33. Two miles north of Mt. Breast, 8 miles south of Banana.
34. One and one-half miles northwest of Consuelo homestead.
35. Condamine fault block, Warwick-Silverwood district.

Superfamily PRODUCTACEA Maillieux, 1941; Cooper, 1944

Diagnosis.—Shells free or attached by spines, pedicle or umbonal cementation. Ornament of spines over part or whole of shell. Concentric and radial ornament varied. Cardinal process and median septum always present. Brachial and marginal ridges variable in development.

Remarks.—Three families and two subfamilies may be recognised within the Productacea, their definition being based on the presence or absence of costation and the distribution of spines. It may be significant that the shell attitude and the mode of attachment adopted by three of the groups during life also differed. Several smaller groups can be recognised within each subfamily, one group in each including genera which are truly representative of the subfamily, the other groups containing less characteristic genera, many of which show affinities with more than one subfamily. These intermediate forms may represent stages in the evolution of the Productacea where major differentiation had only just begun; e.g., *Avonia* and *Protoniella* in the Productellinae have affinities with the Productidae, *Pustula* and *Terrakea* in the Productidae have many strophalosioid characters, and *Aulosteges* and *Juresania* in the Strophalosiinae have productoid affinities.

Family CHONETIDAE Hall and Clarke

Diagnosis.—Large spines along the cardinal margin of the ventral valve. Cardinal area and teeth present. Muscle scars non-dendritic. Fine hair-like spines sometimes developed on the surface of both valves.

Family PRODUCTIDAE Gray, 1840, emend.

Diagnosis.—Costate shells; majority of spines restricted to particular regions of the shell. Adult forms unattached. Dorsal muscle scars dendritic.

Family STROPHALOSIIDAE Stainbrook, 1947, emend.

Diagnosis.—Non-costate in early stages; spines not restricted in areal distribution. Attached by pedicle or umbonal cementation at least for part of their life.

Subfamily PRODUCTELLINAE Schuchert & LeVene, 1929, emend.

Diagnosis.—Attached by pedicle. Shell small, visceral cavity small. Anterior region sometimes weakly costate. Cardinal areas sometimes absent.

Remarks.—This subfamily includes the following genera: *Productella* Hall and Clarke, *Hamlingella* Reed, *Whidbornella* Reed, *Productellina* Reed, *Spinulicosta* Nalivkin, *Leioproductus* Stainbrook, *Productellana* Stainbrook, *Overtonia* Thomas, *Levipustula* Maxwell, *Planoproductus* Stainbrook, *Bispinoproductus* Stainbrook, *Avonia* Thomas and *Protoniella* Bell.

Subfamily STROPHALOSIINAE Schuchert, 1913, emend.

Diagnosis.—Shells attached by umbonal cementation for part of their life. Visceral cavity variable in size. Cardinal areas always present.

REMARKS.—The main group contains *Strophalosia* King, *Leptalosia* Dunbar and Condra, *Heteralosia* King, *Etheridgina* Oehlert, *Spinomarginifera* Huang and *Eostrophalosia* Stainbrook. *Aulosteges* Helmerson, *Wyatkina* Fredericks, *Taeniothaerus* Whitehouse, *Scacchinella* Gemmellaro and *Juresania* Fredericks are less characteristic of the subfamily.

Genus STROPHALOSIA King, 1846

Strophalosia KING, 1846, Annals Mag. Nat. Hist., Ser. I, vol. 18, pt. 5, p. 28; pt. 11, pp. 92–94.
Orthothrix GEINITZ, 1848, Versteinerungen, pp. 14–15.
Wyndhamia BOOKER, 1929, Jour. Royal Soc. New South Wales, vol. 63, pp. 24–32.
Branxtonia BOOKER, 1929, ibid.
Strophalosia King, PRENDERGAST, 1943, Jour. Royal Soc. W. Australia, vol. 28, pp. 37–41.

Diagnosis.—Concavo-convex to plano-convex, sometimes geniculate; small to medium in size. Areas on both valves, dorsal area small. Teeth and sockets always present. Cardinal process trifid. Muscle scars non-dendritic. Brachial, cardinal and marginal ridges developed to varying degrees. Ornament lamellose, spinose, non-costate. Spines on both valves, usually sparse on the dorsal valve. Cicatrix or umbonal distortion usually apparent.

Taxonomy.—Muenster (1839, p. 65, pl. 4,

figs. 3a, b) described the first strophalosiid species as *Spondylus goldfussi* nov.; Geinitz (1842, pp. 578–579, pl. 10 figs. 12, 13), figured and described *Orthis excavatus* nov., but subsequent authors identified his original specimen as belonging to *S. goldfussi*. The name *Strophalosia* was first mentioned by King (1844, p. 313) "for a Productus like shell with an area and possessing a condyloid hinge as in Terebratulas and not a simple one as in the true Productuses." De Verneuil (1844, p. 30) listed "*Productus Morrisianus* King MS., *Productus spiniferus* King MS" in the species of *Productus* Sowerby, and de Verneuil and Murchison (1845, I, p. 223, II, pp. 274, 281), relisted these names and referred to King's manuscript species in the discussion of *Productus horrescens* and *P. cancrini*.

King (1846, pp. 26–42, 93–94) described *Strophalosia* and *S. gerardi*, and included the following species in the genus: "*Productus horrescens* Verneuil; *P. subaculeatus* Murchison; *Orthis productoides* Murch; a Himalayan fossil; three magnesian limestone species found in the neighbourhood of Sunderland, and a few doubtful forms as *Productus spinulosus*." Two of the magnesian limestone species, *S. spinifera* and *S. morrisiana* (listed on p. 28), were not described by King until 1848, and in the meantime they were described by de Koninck (1847, p. 150), as *Productus lewisianus* (=*S. spinifera* King), and by Howse (1848, p. 257) as *Productus spiniferus* (=*S. morrisiana* King), respectively. The third magnesian limestone species to which he referred was identified as *S. goldfussi* by King in 1850 (p. 97, footnote).

Since neither *S. morrisiana* King nor *S. spinifera* King was valid in 1846, and since *S. goldfussi* was not mentioned by name in the 1846 publication, then in accordance with Article 30, II, e, of the International Rules of Zoological Nomenclature, none of these species are eligible for selection as the genotype. The same rule excludes *Productus spinulosus* from consideration. *P. subaculeatus* and *P. productoides* belong to *Productella* Hall, and *P. horrescens* to *Aulosteges* Helmerson, both of these genera being distinct from *Strophalosia*. Thus, under the Rules, *S. gerardi* is the only species eligible for selection. It was erected on two incomplete specimens from an obscure locality in the Himalaya Mountains, and the possibility of obtaining more specimens from that locality is slight. Thus there are strong reasons for recommending the suspension of the Rules in order to designate as the type species, one which is more suitable than *S. gerardi*.

Geinitz (April 1848, p. 14, pl. 5) erected the genus *Orthothrix* (which is a synonym of *Strophalosia*) and *O. lamellosus*, and redescribed *O. excavatus* and *S. goldfussi*. The three species were redescribed by Geinitz in 1861 (pp. 93–101). In both publications, Geinitz figured two species under the name *O. excavatus*, viz.—*S. lewisiana* de Koninck and *S. goldfussi* Muenster. His contemporary authors recognised this error, and all except King (1850, p. 99), rejected the name *O. excavatus* as a synonym of *S. goldfussi*. King (1850), while stating that Geinitz's original specimen, as well as some figured in later publications belonged to *S. goldfussi*, used the name *O. excavatus* to replace *S. spinifera* King (1846, 1848), placed *S. lewisiana* in its synonymy and selected "*Orthis excavatus* Geinitz=*S. spinifera* King" as the genotype of *Strophalosia*. Since *O. excavata* was never a valid species, and since it was not mentioned in King's original publication (1846), then its selection as genotype added further confusion to the already complex problem.

Davidson (1858) reviewed the taxonomy of the genus, rejected *O. excavatus* Geinitz, and placed *S. morrisiana* King (1848) in the synonymy of *S. lamellosa* Geinitz. He did not indicate which was the type species. The majority of subsequent authors (Diener 1911, Etheridge sr. 1872, Etheridge jr. 1880, 1884, 1892, 1914, Girty 1909, Hinchey and Ray 1935, Kirkby 1867, de Koninck 1877, Licharew 1913, 1934, 1936, Malzahn 1937, Reed 1927, 1931, 1944, Trechmann 1945, Waagen 1884), have avoided this question, some have cited *O. excavatus* Geinitz (Schuchert and LeVene 1929, Dunbar and Condra 1932, Prendergast, 1943) and others have cited or figured *S. goldfussi* (Quenstedt 1871, 1885, Gaudry 1883, Koken 1896, Zittel 1913).

Of the three species on which King interpreted the genus, the validity of only one, *S. goldfussi* Muenster, has been accepted

unanimously by subsequent workers, while *S. lewisiana* de Koninck (=*S. spinifera* King) and *S. morrisiana* King, 1848, have been reduced to varietal status by some workers and rejected as synonyms of *S. goldfussi* and *S. lamellosa* by others. *Orthis excavatus* has been used loosely by various authors to include *S. goldfussi* and *S. lewisiana*. In view of this and of the fact that so little is known of *S. gerardi* King, it is suggested that *S. goldfussi* is the species most suited for designation as the type of *Strophalosia*, and that suppression of the trivial name "*excavata*" would help to relieve some of the confusion that has arisen since its erection. Recommendations of this nature will be submitted to the International Commission on Zoological Nomenclature.

Two synonyms of *Strophalosia* are *Branxtonia* and *Wyndhamia*, both erected by Booker (1929, pp. 24–32). Examination of his type material has shown that they are true strophalosiids, and that the three species which he differentiated are conspecific. The characters and taxonomy of this group are discussed under *Strophalosia typica* Booker, later in this paper.

Stratigraphical Distribution.—Except for certain American forms, the majority of strophalosiid species are restricted to the Permian faunas. In India they are most abundant in the lower and middle *Productus* limestones of the Salt Range, where the following species, have been found: *S. costata* Waagen, *S. lewisiana*, *S. tenuispina* Waagen, *S. nodosa* Waagen, *S. plicosa* Waagen, *S. fugax* Reed, *S. sublamellata* Reed and *S. densispinosa* Reed. The fauna of the upper *Productus* limestones is considerably reduced, the main species being *S. indica* Waagen and *S. rarispina* Waagen. Reed (1932), described the Kashmir forms *S.* cf. *S. gerardi* and *S.* cf. *S. clarkei* from the Agglomeratic slate which has been correlated with the Punjabian series below the *Productus* limestone series of the Salt Range. *S.* cf. *S. indica* and *S. costata* have been described by the same author (1933), from the Southern Shan States, *S. proxima* from Yunnan (Reed, 1927), and *S. rarispina* from Indochina, in beds equivalent to the middle *Productus* limestone (Grabau, 1931, pp. 464–465). In China, the species *S. costata* and *S. plicatifera* have been recorded by Chao (1928), from the lower Wunshan limestone. Broili (1916, p. 27), described *S. indica* from the Basleo beds in Timor, these beds having been correlated by Teichert (1941), with the Kungurian of Russia and with the middle *Productus* limestone of the Salt Range. In Russia, the species *S. tholus* Netschajew occurs in the Kazan region, in the lower part of the Kazanian stage. *S. indica* and *S. tholus* have been recorded from

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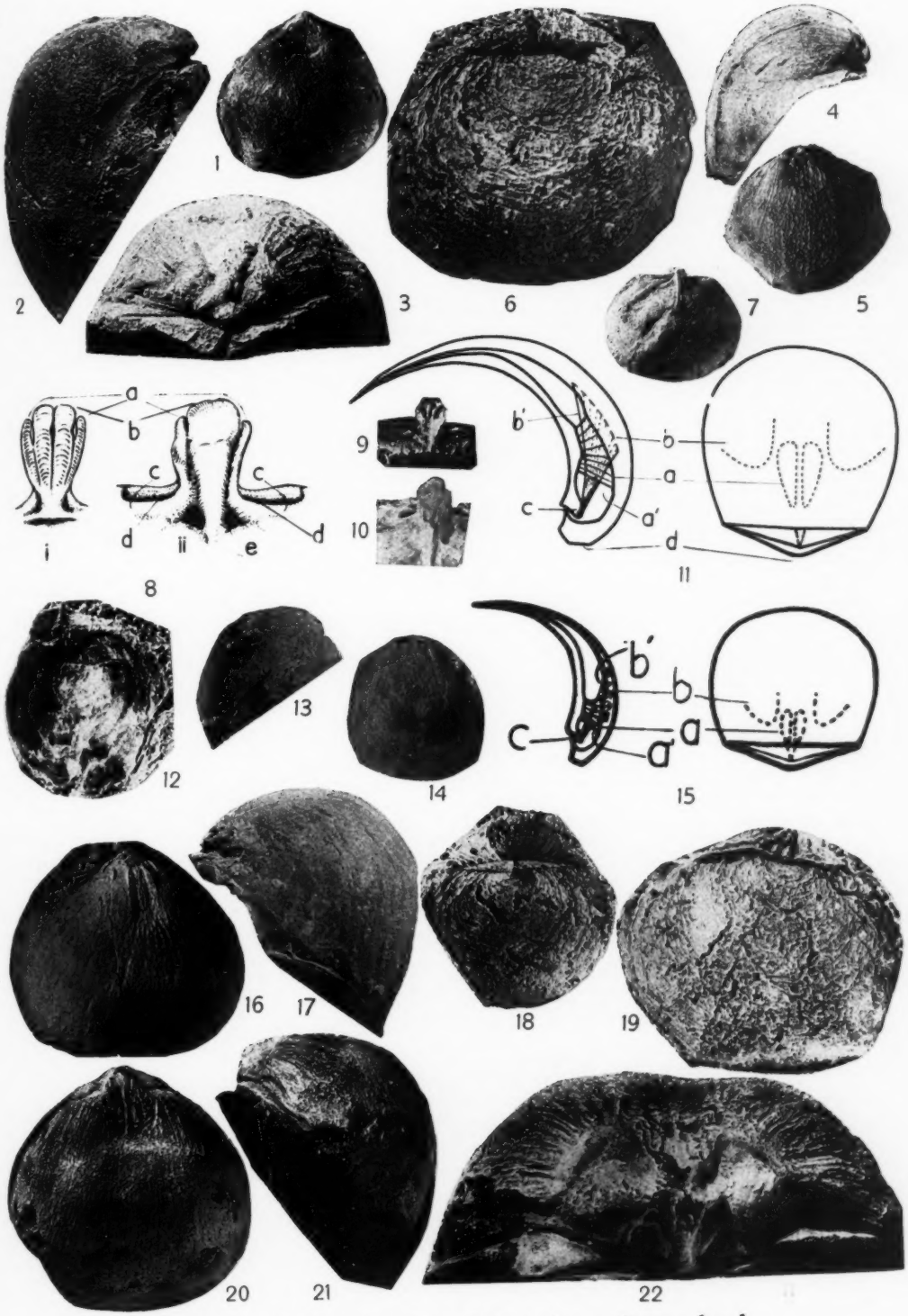
EXPLANATION OF PLATE 54

FIGS. *1–11*—*Strophalosia preovalis* Maxwell, n.sp. *1*, holotype; ventral view of internal cast of ventral valve, UQ F15622, ×0.9, from Cattle Creek beds, Springsure district. *2*, *3*, lateral and posterior views of same specimen, ×1.4. *4*, *5*, ventral and lateral views of internal cast of ventral valve, GSQ F2022, ×0.9, from Homevale. *6*, external mould of dorsal valve, UQ F15625, ×1.4, from Cattle Creek. *7*, dorsal valve, internal, UQ F15620, ×0.9, from Cattle Creek. *8*, dorsal and ventral aspects of the cardinal process, ×8; a=lateral lobes, b=median lobe, c=cardinal process, d=dental sockets, e=base of median septum. *9*, *10*, dorsal and ventral views of the cardinal process, UQ F15623, ×3, from Cattle Creek. *11*, shell profile and outline, and relative positions of the muscles; a=adductor scar, a′=adductor muscle, b=diductor scar, b′=diductor muscle, c=cardinal process, d=umbonal cicatrix. (p. 542)

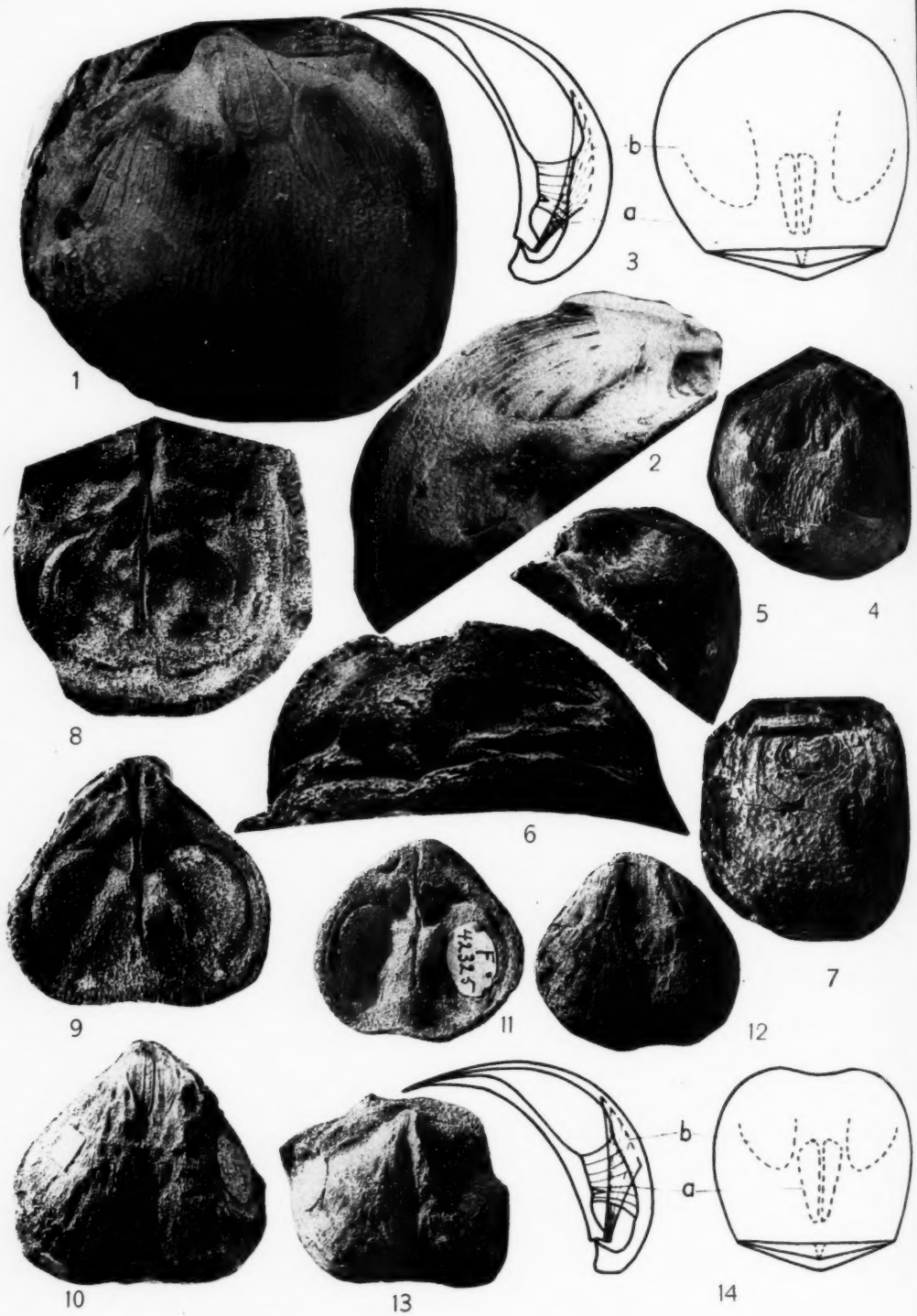
12–15—*Strophalosia preovalis* var. *pristina* Maxwell, n. var. *12*, holotype; dorsal valve and ventral area, GSQ F2093, ×1.4, from Dilly, Springsure. *13*, *14*, lateral and ventral views of the internal cast of the ventral valve, GSQ F2088, from Dilly, ×0.9. *15*, shell profile and outline; a,a′=adductor scar and muscle, b,b′=diductor scar and muscle, c=cardinal process. (p. 543)

16–19—*Strophalosia preovalis* var. *warwicki* Maxwell, n. var. *16*, *17*, holotype; ventral and lateral views of internal cast of ventral valve, UQ F15626, ×1.4, from Stanthorpe Road fault block. *18*, external mould of the dorsal valve and the ventral umbonal cicatrix, UQ F15627, ×1.4, same locality. *19*, dorsal valve, UQ F15629, ×1.4, same locality. (p. 543)

20–22—*Strophalosia brittoni* Maxwell, n. sp. Holotype; ventral and lateral views of internal cast of ventral valve, ×0.9, and posterior view, ×1.4, UQ F15657, from 4 miles SW of Eungella station, Bowen district. (p. 543)



Maxwell, Permian *Strophalosia* from Queensland



Maxwell, Permian *Strophalosia* from Queensland

the Kharaulakh River and Mountains, and *S. tholus* has been described from the Pinega Zechstein of northern Russia by Mircink (1938), and Grabau (1931). Licharew (1936), described *S. netschajewi* from the Lyttonia limestone and *S. rugosocostata* from beds of Upper Permian age in the Caucasus. *S. praepermica* Gerassimov has been recorded from the *Schwagerina* limestone of Upper Carboniferous age. Tolmachoff (1915, p. 34), described *S. grandis* from the Kolyma River, Siberia, and Licharew (1934) described *S. sibirica*, also from the Permian of Siberia.

In Western Europe, the main development of the genus is found in the Zechstein and the Magnesian limestone, the most abundant species being *S. goldfussi. S. lamellosa*, *S. lewisiana* and *S. productiformis* Schauroth. The North American faunas do not contain many representatives of the genus. Girty (1909, pp. 276–277), described the species *S. hystricula* and *S. cornelliana* Derby from the Gaudalupian faunas of Texas. The subgenera *Heteralosia* and *Leptalosia* were prolifically developed during the Pennsylvanian, but there was a dearth in strophalosiid faunas during Permian times. R. E. King (1930, p. 96), in discussing the faunas of the Glass Mtns., Texas, observed "The group of shells to which the name *Strophalosia* is generally applied may not be congeneric with the genotype of *Strophalosia*, in which case, a new name must be found for the group." Hinchey and Ray (1935, pp. 247–250), described three species from the Warsaw formation of St. Louis County, Mo., assigning them to *Strophalosia. S. butlerensis*, described by Stainbrook from the Mississippian Alpington formation of Iowa, has marked productelloid affinities. The American species are very different from those of Eurasia and Australia.

In Australia, the genus is most abundant in those formations which have been correlated with the Artinskian and Kungurian of Russia. The eastern Australian species have been found in the upper and lower Marine series of New South Wales, the Cascades stage in Tasmania, and in Queensland in beds ranging from the Dilly to the Mantuan Downs *Productus* bed. Species described by Prendergast (1943) from the western Australian faunas include *S. clarkei* from the Gascoyne series, *S.* cf. *S. beecheri* from the Callytharra limestone, *S. etheridgei* from the Fossil Cliff horizon and the Wandagee stage, *S. jukesi* from Talbot's Cairn, *S. kimberleyensis* and *S. multispinifera* from the Nooncoonbah series and *S. tenuispina* from the Fossil Cliff horizon. Teichert (1947, p. 28), determined the age of these formations as Artinskian.

The species of *Strophalosia* are neither wide ranging stratigraphically, nor widespread geographically, and comparsion of the forms from the different countries does not always result in successful correlation. With the possible exception of *S. gerardi* King and *S. lewisiana* de Koninck, the species are comparatively restricted. Waagen (1884, pp. 640–641) noticed this feature in the Salt Range faunas. The strong differences between the eastern and western Australian faunas, and the lack of European and American elements in the Queensland faunas is significant.

In Australia the genus is restricted to the Permian, its approximate range being from Sakmarian into Kungurian. In Russia it is

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EXPLANATION OF PLATE 55

FIGS. *1–3*—*Strophalosia brittoni* Maxwell, n. sp. *1, 2*, ventral and lateral views of internal cast of the ventral valve, UQ F16258, ×1.3, from Homevale station. *3*, shell profile and outline; a = adductor scar, b = diductor scar. (p. 543)

4–7—*Strophalosia brittoni* var. *gattoni* Maxwell, n. var. *4, 5, 6*, holotype; ventral and lateral views of internal cast of ventral valve, ×0.8, and posterior view, ×1.3, UQ F15655, from Gattonvale outstation, Bowen district. *7*, external mould of dorsal valve, UQ F15656, ×0.8, same locality. (p. 544)

8–14—*Strophalosia typica* Booker. *8*, internal cast of the dorsal valve, AM F39440, ×0.8, from Por. 147, Par. Branxton, County Northumberland, New South Wales. *9, 10*, dorsal and ventral views of internal cast of shell, AM F42325, ×0.8; same locality. *11, 12*, holotype; dorsal and ventral views of internal cast of shell, AM F41763, ×0.8, same locality. *13*, internal cast of ventral valve, AM F41766a, ×0.8, same locality. *14*, shell profile and outline; a = adductor scars, b = diductor scars. (p. 545)

well represented in the Kazanian, and species have been recorded from the early Mississippian of America.

STROPHALOSIA PREOVALIS Maxwell, n. sp.
Plate 54, figures 1–11

Holotype.—UQ F15622, from Cattle Creek, 2 miles upstream from its junction with Consuelo Creek, Springsure district, central Queensland.

Horizon.—Cattle Creek beds.

Diagnosis.—Shell small, dorsal valve geniculate, trail of medium length. Shell outline subcircular. Cardinal area at a low angle to the plane of the shell. Dorsal spines sparse. Ventral adductor platform short and low; teeth and dental callosities small, posterior wall low. Median septum long and high.

Description.—External: The shell is concavo-convex, non-sinuate, the dorsal valve geniculate. A high, slightly incurved umbo is developed, and the ventral area rises at a low angle from the plane of the shell. A small cicatrix deforms the umbo. The dorsal cardinal area is extremely low. Concentric growth lamellae and stronger wrinkles are abundant, particularly on the dorsal valve. Spines are abundant on the ventral valve but vary in intensity on the dorsal. In the region of geniculation, small radial puckers in the shell substance give the appearance of incipient costae.

Internal, ventral valve: The adductor muscle platform is short and low. The scars are tear-shaped and smooth, except for weak concentric markings which probably represent growth lines. The diductor scars occupy depressed areas which are longitudinally striated and almost circular in outline. Two small teeth project anterodorsally from the delthyrial corners and supporting dental callosities are weakly developed. The posterior wall of the delthyrial region is low and semispherical, and there is little thickening of the umbonal walls. The internal surface is comparatively smooth.

Dorsal valve: The curvature of the internal surface is less than the external concavity, the thickening of the anterior margin resulting in a sharp geniculation. The cardinal process rises sharply, and is separated from the median septum at its base by a shallow depression. Cardinal ridges merge into the base of the process and appear to continue as the lateral lobes which curve posterodorsally. The lateral lobes become more strongly curved and separated from the central portion of the process during ontogeny. The adductor muscle scars are non-dendritic and are differentiated into anterior and posterior elements. The anterior element is formed on a low elevation and is subtriangular in outline, while the posterior element, which is on a lower surface, is wider and less elongate. They are situated in front of the cardinal ridges which diverge from the base of the cardinal process and extend laterally for two thirds the width of the hinge, making an angle of approximately 30° with it. The median septum, which is highest near the base of the cardinal process, terminates near the centre of the valve. Brachial ridges are weakly developed and in most cases are indistinct.

Dimensions.—	Holotype (mm.)	Topotypes (mm.)		
Maximum width	29.5	24	21	18.5
Height, dorsal	—	19.5	—	18.5
Height, ventral	23.5	22.0	16.0	—
Width of hinge	15.0	14.0	—	12.5
Length of ventral adductor scar	8.0	—	5.0	—
Overlap of diductor scars	4.5	—	4.5	—
Distance of adductor scar from apex	6.0	—	4.0	—
Width/height, dorsal	—	1.23	—	1.0
Width/height, ventral	1.26	1.09	1.31	—
Width/hinge-width	1.96	1.72	—	1.48

Remarks.—Analysis of the dimensions and proportions of this species has shown that no simple growth ratio exists between the size of the shell and the dimensions of the muscle scars and the cardinal process. The external proportions show little variation during ontogeny. The spinosity of the dorsal valve varies in intensity and in some individuals is completely suppressed. The inconstant nature of their development suggests that dorsal spines may have been readily influenced by environment.

This species occurs in the Cattle Creek beds in the Springsure district; in the Homevale-Mt. Britton beds, Yatton limestone, and lowest Cracow beds on the eastern margin of the Bowen basin; in the *Springsurensis* limestone of the Yarrol basin; in the earliest fossil horizon of the Cressbrook fault block; in the *Eurydesma* beds of the

Stanthorpe Road fault block; and at Kimbriki in northern New South Wales.

Range.—The age of the Cracow fauna in which this species occurs has been determined as Sakmarian and early Artinskian by Hill (1950).

STROPHALOSIA PREOVALIS var. PRISTINA Maxwell, n. var.
Plate 54, figures 12–15

Holotype.—GSQ F2093; found in the Dilly beds, 2 miles north of the Dilly railway station, Springsure district.

Diagnosis.—As for species; smaller dimensions, less transverse shell, wider hinge, stronger area, more primitive teeth.

Description.—This variety closely resembles the younger species except for its external proportions. The shell is small and concavo-convex, the concavity of the dorsal valve being weak. The ventral area is comparatively high and curved, and is almost in the plane of the shell. The dorsal area is minute. Both valves are spinose, the dorsal spines being sparse. Due to the manner of preservation, internal structures are difficult to determine. The umbonal region of the shell is weakly thickened, its contour resembling that of the species. A strong cardinal process and a short low adductor platform are developed.

Dimensions.—	Holotype (mm.)	Topotypes (mm.)		
Maximum width	13.0	9.5	21.0	12.0
Height, dorsal	11.0	8.5	15.0	8.5
Height, ventral	13.0	—	19.0	11.0
Hinge-width	8.0	7.0	14.0	8.0

Remarks.—Widest variation in this form is found in the proportions of the dorsal valve, the relative length of the valve decreasing during ontogenetic development, while the overall proportions of the shell are maintained by corresponding increases in the height of the ventral area, and in the degree of umbonal incurvature. This variety has been found in the Dilly beds, which are slightly older than the Cattle Creek beds of Sakmarian-Artinskian age. The only species from foreign faunas which has similar proportions is *S. nodosa* Waagen (1884, pp. 652–653), which was recorded from the *Chonetes* bed in the lower *Productus* limestone at Amb, in the Salt Range, India.

STROPHALOSIA PREOVALIS var. WARWICKI Maxwell, n. var.
Plate 54, figures 16–19

Holotype.—UQ F15626; from the *Eurydesma* beds, Stanthorpe Road fault block, between Cardiomorpha and *Eurydesma* Gullies, Por. 192, Parish of Wildash.

Diagnosis.—As for species, but cardinal areas higher, umbonal cicatrix stronger, hinge wider; dorsal valve more transverse; ventral proportions and muscle scars as for species; moderate umbonal thickening.

Description.—The distinguishing features of this variety are its large umbonal cicatrix, well developed cardinal areas, and the slightly thickened walls of the umbonal region. This thickening has resulted in the umbonal cavity being less evenly curved, the floor being almost flat. The distribution of the internal characters is almost identical with that of the species, although the ventral adductor scar tends to be longer and narrower. Radial striae are developed on the dorsal valve.

Dimensions.—	Holotype (mm.)	Topotypes (mm.)		
Maximum width	25.0	22.0	22.0	16.0
Height, dorsal	—	—	17.5	12.0
Height, ventral	23.0	18.0	—	—
Hinge-width	14.5	12.5	12.0	12.5
Length of ventral adductor scar	7.0	5.5	—	—
Overlap of diductor scars	4.0	3.0	—	—
Distance of adductors from apex	4.5	3.0	—	—
Width/height, dorsal	—	—	1.26	1.33
Width/height, ventral	1.09	1.22	—	—
Width/hinge-width	1.65	1.76	1.83	1.21

Remarks.—The dimensions and proportions of this variety are very similar to those of the species s.s. It may represent an evironmental modification of the species or it may have evolved at a slightly different stage in the "*preovalis*" plexus. The variety has been found in the fault blocks of Stanthorpe Road and Cressbrook, and at Kimbriki in New South Wales.

STROPHALOSIA BRITTONI Maxwell, n. sp.
Plate 54, figures 20–22; Plate 55, figures 1–3

Holotype.—UQ F15657; from the Mt. Britton-Homevale beds, 4 miles south west of Eungella station, Bowen district.

Diagnosis.—Ventral valve large, strongly convex, weakly sinuate; hinge narrow. Maximum width greater than height of shell. Dorsal valve moderately concave. Cardinal area strongly curved, at high angle to the plane of the shell. Ventral adductor platform long, of medium height. Teeth strong, supported by heavy callosities; high, flat posterior wall.

Description.—External: The ventral valve is strongly convex and sometimes weakly sinuate, although the median section tends to be flat. The hinge is narrow, the umbo well incurved, and the cardinal area which is concave rises at a high angle from the plane of the shell. The dorsal valve is moderately concave, and develops a weak geniculation. Growth lamellae and spines vary in intensity on both valves.

Internal: Two strong teeth, supported by bulbous dental callosities are the most distinctive features of this species. The posterior wall of the delthyrial region is extremely high and flat, but shell thickening has destroyed the even curvature of the remaining part of the umbonal region. The ventral adductor platform is moderately high and long, and is partly enclosed by large depressions which carry the diductor scars.

Dimensions.—	Holotype (mm.)	Topotype (mm.)
Maximum width	45.0	49.5
Height, ventral	39.0	45.0
Hinge-width	26.5	25.0
Length of ventral adductor scar	11.0	13.0
Overlap of diductor scars	7.0	9.5
Distance of adductors from apex	11.0	12.0
Width/height, ventral	1.15	1.10
Width/hinge-width	1.70	1.98

Remarks.—This species is characterised by the strong development of its posterior internal structures. It has been found only in the eastern part of the Bowen syncline, where it is associated with *S. preovalis*. It is particularly abundant at Homevale. Present evidence suggests that *S. brittoni* is the parent species of *S. typica*, *S. clarkei* and *S. brittoni* var. *gattoni*, these forms appearing in the Ingelara beds and their equivalents. Their evolution consisted in the modification of the posterior structures of the ventral valve, the degree of convexity of this valve and in one case, the development of sinuation.

Range.—The species sensu stricto occurs only in the Mt. Britton-Homevale beds, of Sakmarian or early Artinskian age.

Strophalosia brittoni var. gattoni Maxwell, n. var.
Plate 5, figures 4–7

Holotype.—UQ F15655; found in the lower part of the Big *Strophalosia* bed, middle Bowen series, at Gattonvale outstation, Collinsville district.

Diagnosis.—As for species. Non-sinuate; dental callosities, teeth and posterior wall of delthyrial cavity smaller. Heavy shell thickening in the umbonal walls.

Description.—External: The ventral valve is strongly convex and non-sinuate. It is subquadrate in outline, being slightly wider than high, with a narrow hinge. The umbo is incurved over a high curved area which rises from the plane of the shell at a moderate angle. Other characters are similar to those of the species s.s.

Internal, ventral valve: The large teeth and dental callosities, although characteristic of this variety, are not as strong as those of the species s.s. Shell thickening in the umbonal walls is marked. The ventral adductor platform is moderately high and long, carrying two very narrow scars. The diductor scars occupy large, shallow depressions, but are never sharply defined. Growth lamellae and pallial markings are apparent on the remaining surface.

Dorsal valve: The characters of this valve are not specifically diagnostic. The median septum extends anteriorly for more than half the valve length. Cardinal, marginal and brachial ridges are weakly developed, and the adductor scars which are differentiated into anterior and posterior elements, occupy low platforms. The cardinal process is of medium size.

Dimensions.—	Holotype (mm.)	Topotypes (mm.)	
Maximum width	40.0	40.0	41.0
Height, dorsal	—	—	—
Height, ventral	35.0	34.5	37.0
Hinge-width	18.0	16.0	20.0
Length of ventral adductor scar	11.5	13.5	13.0
Overlap of diductor scars	6.5	7.5	7.0

Dimensions.—	Holotype (mm.)	Topotypes (mm.)	
Distance of adductor from apex	9.5	12.0	8.0
Width/height, ventral	1.14	1.16	1.11
Width/hinge-width	2.22	2.50	2.05

Remarks.—Comparatively wide variation occurs in the height of the posterior wall and the size of the dental callosities. However, these characters are always diagnostic of the variety. Individuals intermediate in character between it and *S. clarkei* have been found, thus suggesting that the two forms may be conspecific. However the majority of individuals resemble one or the other, and the occurrence of so few intermediate forms does indicate a divergence of trends. *S. brittoni* var. *gattoni* is restricted to the lower part of the Big *Strophalosia* bed, whereas *S. clarkei* occurs throughout the whole of this bed, although it decreases in abundance towards the top.

Range.—This variety occurs in that part of the Big *Strophalosia* bed which has been correlated with the Ingelara beds, the age of which is probably Kungurian.

STROPHALOSIA TYPICA Booker, 1929
Plate 55, figures 8–14

Wyndhamia dalwoodensis BOOKER, 1929, Jour. Royal Soc. New South Wales, pp. 25–26, pl. 1, figs. 1–5, pl. 3, figs. 5–7.
Wyndhamia valida BOOKER, 1929, ibid., pp. 26–28, pl. 2, figs. 1–5.
Branxtonia typica BOOKER, 1929, ibid., pp. 30–31, pl. 3, figs. 1–3.

Holotype.—Here selected: AM F41763; from 2,250 feet below the Muree beds, Branxton stage, upper Marine series, at Port. 147, Parish Branxton, County Northumberland, N.S.W.

Diagnosis.—Large shell, ventral valve moderately convex, strongly sinuate; dorsal valve flat to weakly concave, geniculate. Slightly wider than long; hinge wide. Cardinal areas of medium dimension, ventral area in plane of shell or sloping posteroventrally. Ventral adductor platform long, moderately high.

Description.—External: The dorsal valve varies from weakly convave to flat, while the ventral valve is moderately convex and sinuate. The umbo is weakly incurved, the cardinal area being almost in the plane of the shell. In some cases, it slopes posteroventrally from the hinge. The shell is wider than long, and has a wide hingeline. Concentric growth lamellae and spines are irregularly distributed over the shell, the spines of the dorsal valve being less abundant.

Internal, ventral valve: The adductor muscle platform is long and of medium height. It is overlapped for more than half its length by the diductor scars which are weakly impressed. Two strong teeth and dental callosities and thickening of the shell wall characterise the umbonal region.

Dorsal valve: A comparatively strong, bulbous cardinal process is supported by a large median septum and cardinal ridges. The adductor muscle scars are smooth, posteriorly sloping elements, the anterior ones being longitudinally triangular and the posterior ones being transversely trapezoidal in outline. The brachial ridges diverge from the junction of the posterior and anterior elements. Vascular markings occur along the anterior and antero-lateral margins.

Dimensions.—	Holotype (mm.)	Topotypes (mm.)		
Maximum width	34.0	26.0	40.0	42.5
Height, dorsal	28.0	—	34.0	35.0
Height, ventral	33.5	24.5	—	40.5
Hinge-width	—	21.5	26.0	—
Length of ventral adductor scar	14.0	11.0	—	13.5
Overlap of diductor scars	8.5	6.5	—	8.5
Distance of adductor from apex	6.0	4.0	—	—
Width/height, dorsal	1.21	—	1.18	1.21
Width/height, ventral	1.01	1.06	—	1.06
Width/hinge-width	—	1.21	1.54	—

Remarks.—a. Taxonomy. Booker (1929, pp 24–32) erected the subgenera *Wyndhamia* and *Branxtonia*, the former as a subgenus of *Strophalosia*, the latter as a subgenus of *Productus*. Examination of his type material has shown that the three species which he described are conspecific, and that they belong to the genus *Strophalosia*. *Wyndhamia* was erected as a subgenus on the basis of its sinuation, coarse ornament and "undifferentiated" dorsal adductor scars (Booker, 1929, pp. 27–28). Sinuation is characteristic of one of the species on which *Strophalosia* was originally inter-

preted by King (1846), coarseness of ornament is not a significant character, and further, the dorsal adductor scars of Booker's type material are differentiated. *Branxtonia* is identical with *Wyndhamia*, but was erected to include forms which, through their manner of preservation, had the appearance of having narrow hinge lines and no ears. The type material is preserved as impressions, and on internal casts of the whole shell the ears cannot be preserved, due to the close contact of the two valves in the auricular regions. After examining the type material, the conclusion was reached that it represents only one species of *Strophalosia*, this species being closely related to *S. brittoni* and *S. clarkei*.

b. Variation. This species shows little variation within individual communities, but differences due to geographical distribution are noticeable. Specimens of the species from the Ingelara beds are distinguished from the southern forms by their smaller dimensions, more transverse outline, weaker convexity and reclined cardinal area.

c. Related species and varieties. The species has close affinities with both *S. clarkei* and *S. brittoni*. It has probably evolved from the latter, developing new contour and shape, but retaining the same umbonal structures—large dental callosities and teeth. *S. clarkei*, on the other hand, retained somewhat similar shape, but modified its umbonal structure.

d. Occurrence. *S. typica* has been found only in the Branxton stage in New South Wales and the Ingelara beds and their equivalents in Queensland. These beds have been determined as late Artinskian-early Kungurian in age (Teichert and Fletcher 1943; Campbell 1951). The species figured by Prendergast (1943, pl. 5, figs. 18–20) as *S. jukesi*, from the Wooramel River district of Western Australia, is more similar to *S. typica* than to the type specimens of *S. jukesi* Etheridge.

STROPHALOSIA CLARKEI Etheridge, sr.
Plate 56, figures 1–7

Productus clarkei ETHERIDGE, 1872, Quart. Jour. Geol. Soc. London, vol. 28, p. 334, pl. 17, figs. 2, 2a, b; pl. 18, figs. 4, 4a.

Productus clarkei Etheridge, DE KONINCK, 1887, Mem. Soc. Sci. Liege, vol. 7, p. 203, pl. 10, fig. 5; pl. 11, fig. 3.

Productus clarkei Etheridge, ETHERIDGE, JR., 1878, Cambridge, p. 51.

Strophalosia clarkei Etheridge, PRENDERGAST, 1943, Jour. Royal Soc. W. Australia, vol. 28, pp. 42–43, pl. 5, fig. 4.

Holotype.—Here selected: QM F2887, Daintree collection; figured by Etheridge, sr. (1872, pl. 17, fig. 2). From the Collinsville area, Bowen basin. (The matrix in which the holotype is preserved is similar to that from Gattonvale where the lower part of the Big *Strophalosia* bed is exposed.) It seems then that the holotype was collected from the lower part of the bed.

Diagnosis.—Ventral valve large, moderately convex; dorsal valve weakly concave to flat. Width greater than height; hinge narrow. Ventral cardinal area at low angle to plane of the shell. Ventral adductor platform long and moderately low; teeth and dental callosities medium to large; posterior umbonal wall low, and sloping posteroventrally. Cardinal process heavy, boss-like. Internal surface of varied relief; strong anterior ridge, high muscle platform.

Description.—External: The ventral valve is usually low, evenly convex, with a slight median flattening, which becomes an incipient sinus in aberrant forms. The cardinal area is of medium height, gently curved and almost in the plane of the shell. The dorsal valve varies from flat to weakly concave. Growth lamellae are abundant, particularly on the dorsal valve. Spines are never numerous.

Internal, ventral valve: This valve is distinguished by the medium to large dental callosities, the sloping posterior wall, and the comparatively low, long adductor muscle platform. There is a minimum of shell thickening in the umbonal region, and the diductor muscle scars are but weakly impressed.

Dorsal valve: The internal surface of this valve tends towards flatness, although strong marginal and anterior ridges are developed. In extreme cases these ridges form high lips. The cardinal process is a heavy, boss-like structure projecting ventrally rather than postero-ventrally. The median septum extends for two thirds of the valve length, and becomes higher anteriorly. The adductor scars are strongly impressed on dome-like elevations, and brachial ridges

diverge from the junction of the posterior and anterior elements.

Dimensions.—	Holotype (mm.)	Topotype (mm.)
Maximum width	46.0	43.5
Height, dorsal	—	34.6
Height, ventral	38.2	—
Hinge-width	31.6	31.2
Length of ventral adductor scars	16.0	—
Width/height, dorsal	—	1.25
Width/height, ventral	1.20	—
Width/hinge-width	1.45	1.40

Remarks.—a. Taxonomy. This species, erected by Etheridge, sr., was redescribed by Etheridge, jr. (1880, pp. 27–32), who based his interpretation on the dorsal valves of the correct species and the ventral valves of the species *S. ovalis*, n. sp., which is described in this paper. Three species occur in the Bowen district and examination of Etheridge's (sr.) type material reveals that the one which was described originally as *S. clarkei* is found in the Big *Strophalosia* bed, being most abundant near the base. *S. ovalis* occurs in a younger decalcified sandstone, and has been found only at the one locality, 4½ miles up Parrot Creek. In his description, Etheridge, jr. (1880, p. 29) stated, "This interesting species is known to us under two conditions—internal casts of the ventral valve in sandy mudstones, and dorsal valves retaining more or less of their shelly material. Examples with the valves united I have not seen." The ventral valves which Etheridge figured did not come from the same locality as his dorsal valves.

b. Variation. Excessive development of shelly material is responsible for the wide variation found in this species. It is most marked in dorsal valves of individuals from the higher beds and may represent a form of gerontism or the reaction to unfavourable environment. Other forms develop extremely convex ventral valves, while others develop incipient sinuation and smaller dental callosities. These last forms are found at Gattonvale in the Bowen district, at Ingelara in the Springsure district, and in the Branxton stage at Nowra, New South Wales. The variety *S. clarkei* var. *minima*, described later, occurs in the upper part of the Big *Strophalosia* bed and is intermediate in character between *S. clarkei* and *S. ovalis*. *S. clarkei* is closely related to *S. typica* and *S. brittoni* var. *gattoni*, all three of which represent divergent trends from *S. brittoni* s.s. It is distinguished from these by its contour and umbonal structures. From *S. ovalis* it is distinguished by its less convex ventral valve, less concave dorsal valve, stronger dental callosities and comparatively unthickened shell walls in the umbonal region. These same characters distinguish *S. clarkei* from *S. jukesi*.

c. Correlations. *S. clarkei* ranges throughout the Big *Strophalosia* bed, but is most abundant at its base. The later forms are less numerous and show various morphological modifications. It is found also in the Ingelara beds and the Branxton stage. Its age is approximately Kungurian.

STROPHALOSIA CLARKEI var. MINIMA Maxwell, n. var.

Plate 56, figures 9–11

Holotype.—UQ F16262; from the upper part of the Big *Strophalosia* bed, Bull Creek, Homevale station road crossing, Mt. Britton-Nebo district.

Diagnosis.—Medium sized shells; dorsal valve weakly concave, geniculate; ventral valve of medium convexity, with weak sinuation or medial flattening. Ventral area at low attitude to the plane of the shell. Hinge extremely wide. Ornament strongly lamellose. Dental callosities of medium size; posterior umbonal wall low, sloping posteroventrally; walls heavily thickened. Ventral adductor platform high, of moderate length.

Description.—This variety is distinguished from the species sensu stricto by its smaller dimensions, wider hinge, stronger convexity and internally, by the heavy thickening in the umbonal region, high ventral adductor platform and absence of thickening in the dorsal valve. The size and shape of the dental callosities, the sloping posterior wall, the low attitude of the area and the weak concavity of the dorsal valve reflect its close relation to the species sensu stricto.

Dimensions.—	Holotype (mm.)	Topotypes (mm.)		
Maximum width	33.0	36.7	25.5	28.6
Height, dorsal	—	—	—	23.6
Height, ventral	28.0	28.0	22.7	—
Hinge-width	29.0	33.6	24.7	22.6
Length of ventral adductor scars	7.0	7.9	5.1	—

Overlap of diductors	3.5	3.4	3.0	—
Distance of adductors from apex	4.5	7.5	5.0	—
Width/height, dorsal	—	—	—	1.21
Width/height, ventral	1.19	1.30	1.12	—
Width/hinge-width	1.14	1.09	1.03	1.26

Remarks.—This variety has evolved from *S. clarkei* towards *S. ovalis* by the development of stronger concavo-convexity and by modification of the internal contour of the umbonal region. These features are typically "ovalian," and present evidence suggests that the variety represents a phase in the evolution of *S. ovalis*. It occurs in the Bowen basin at Homevale and 2.2 miles west of the Cracow township, in beds equivalent to the top of the Big *Strophalosia* bed.

STROPHALOSIA OVALIS Maxwell, n. sp.
Plate 57, figures 4–14

Holotype.—UQ F15630; from the Mantuan Downs *Productus* bed, 1½ miles northwest of Consuelo Homestead, Springsure district.

Diagnosis.—Large, concavo-convex, geniculate; visceral cavity of medium size. Shell outline subcircular. Dental callosities weak, rounded. Umbonal walls thickened. Ventral adductor platform high, short to medium in length. Cardinal process and median septum strong.

Description.—External: The shell is concavo-convex, subcircular in outline, with the maximum width anterior to the hinge. Cardinal areas are developed on both valves, the dorsal area being very small and weakly arched. That of the ventral valve is larger, curved and laterally striated. The ventral apex is weakly distorted by a small cicatrix. The umbo is incurved over the ventral area which projects posterodorsally from the plane of the shell. Spines vary in intensity, being most numerous on the ventral valve. Growth lamellae are strongest on the dorsal valve.

Internal, ventral valve: The adductor muscle platform is of medium length, rising anteriorly to a considerable height. The scars are marked by concentric lines, suggesting movement of the muscle attachment during growth. The diductor scars occupy subcircular areas which are impressed into the shell floor, and carry flexuous, longitudinal striations. The uneven surface of the umbonal walls, caused by shell thickening in that region is very noticeable. Strong teeth are developed, but the supporting dental callosities are small.

Dorsal valve: The internal surface of this valve tends towards flatness, the strong curvature of the exterior being masked by heavy marginal thickenings. These have resulted in the development of a sharp geniculation at the anterior margin of the venter. The cardinal process is large, its lateral lobes being strongly curved to produce a claw-like structure. The base of the process is

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EXPLANATION OF PLATE 56

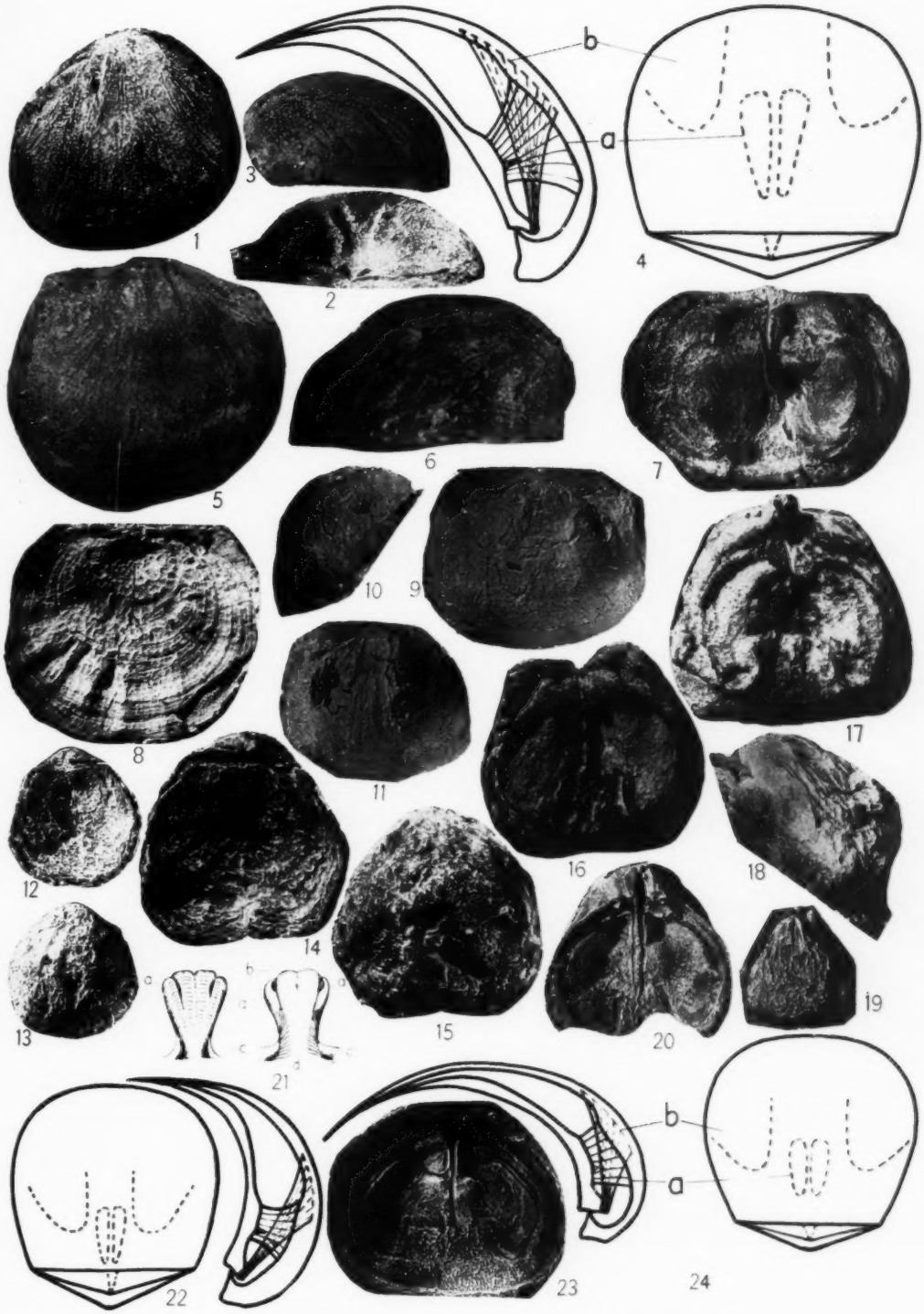
All figures ×1 unless otherwise indicated.

FIGS. *1–7*—*Strophalosia clarkei* Etheridge. *1–3*, ventral, posterior and lateral views of the internal cast of the ventral valve, UQ F16260, from Carpet Snake Creek, Bowen district. *4*, shell profile and outline. *5*, *6*, holotype; ventral and lateral views of partly decorticated ventral valve, QM F2887, from the Bowen River. *7*, dorsal valve, internal, UQ F15643, from Collinsville. *8*, syntype, dorsal valve, QM F2887, from Bowen River. (p. 546)

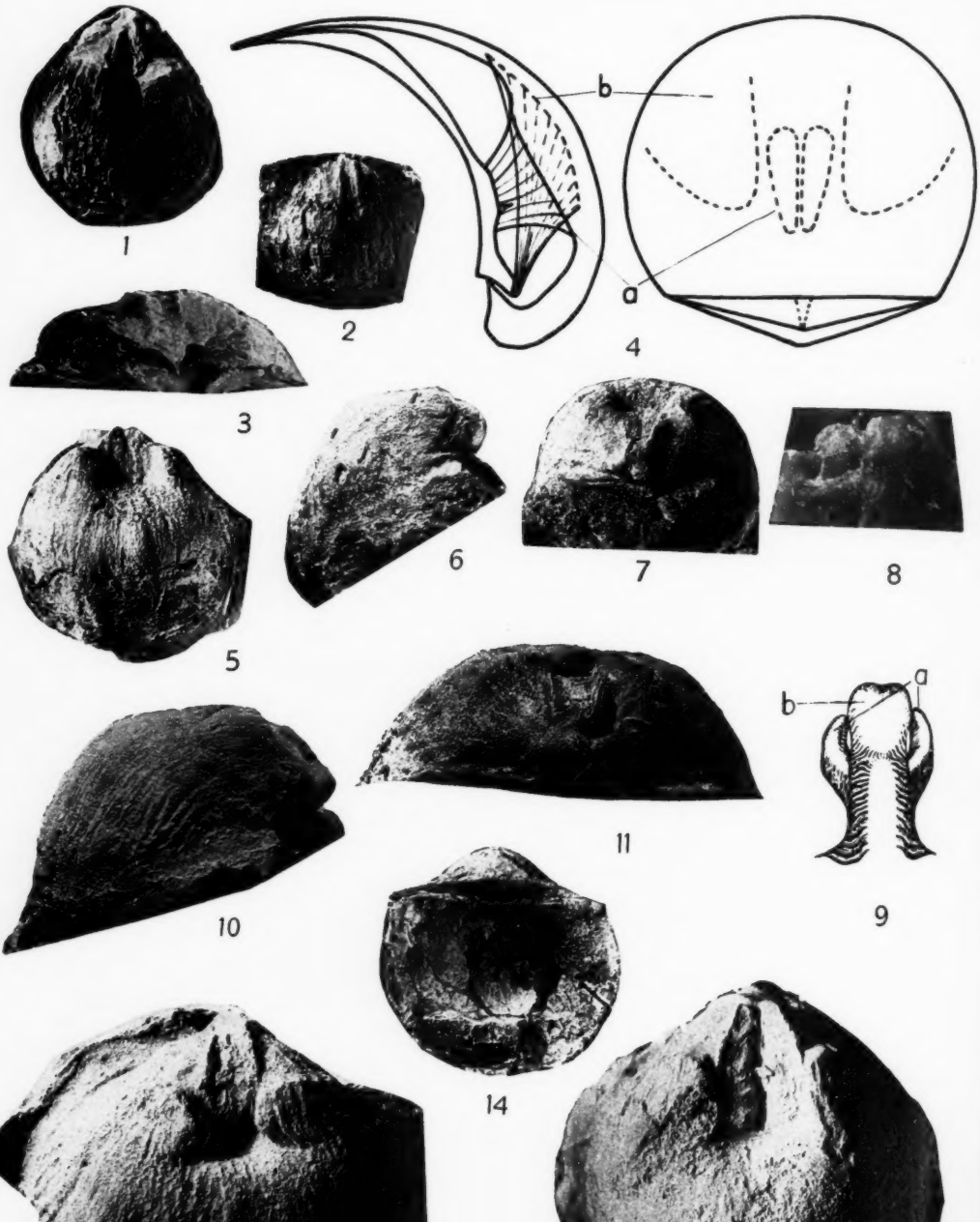
9–11—*Strophalosia clarkei* var. *minima* Maxwell, n. var. *9*, *10*, holotype; ventral and lateral views of internal cast of the ventral valve, UQ F16262, from Bull Creek, Homevale station. *11*, internal cast of the ventral valve, UQ F16263, same locality. (p. 547)

12–22—*Strophalosia jukesi* Etheridge. *12–13*, dorsal and ventral views of UQ F15646, ×0.5, Rathbone Quarry, Granton, Tasmania. *14–15*, holotype, dorsal and ventral views, BMNH BB9807, from Tasmania. *16–17*, syntypes, internal dorsal valves, BMNH BB9806, BB9808, same locality. *18–19*, internal cast ventral valve, lateral view, ×1, and ventral view, ×0.5, UQ F15647, from Huon Road, 2–3 miles from Hobart, Tasmania. *20*, dorsal valve, internal cast, UQ F15649, from same locality. *21*, cardinal process, drawn from UQ F15650, ×2, same locality. *22*, shell profile and outline. (p. 550)

23–24—*Strophalosia jukesi* var. *concava* Maxwell. n. var. *23*, dorsal valve, internal cast, UQ F15642, from Wallaby Rocks, Stanthorpe. *24*, shell profile and outline; a = adductor scars, b = diductor scars. (p. 551)



Maxwell, Permian *Strophalosia* from Queensland



Maxwell, Permian *Strophalosia* from Queensland

buttressed by a long median septum and two cardinal ridges which curve laterally, bordering deep dental sockets. The septum extends anteriorly for more than half the length of the venter. The adductor muscle scars occupy two low elevations which slope towards the cardinal ridges, the posterior slope being steeper than that of the anterior elements. The surface of the scars is non-dendritic. The anterior region of the valve near its geniculation is marked by closely packed, fine radial elevations.

Dimensions.—	Holotype (mm.)	Other Specimens (mm.)			
Maximum width	33.0	31.2	41.0	30.0	40.0
Height, dorsal	—	—	—	25.0	32.0
Height, ventral	29.0	28.0	35.0	—	—
Hinge-width	22.0	19.0	30.0	20.0	24.0
Length of ventral adductors	8.6	10.0	11.0	—	—
Overlap of diductors	4.5	5.2	4.5	—	—
Distance of adductors from apex	10.5	8.5	9.5	—	—
Width/height, dorsal	—	—	—	1.20	1.25
Width/height, ventral	1.16	1.11	1.17	—	—
Width/hinge-width	1.50	1.64	1.37	1.50	1.66

Remarks.—Variation and evolution. As is the case with the other species, the length of the ventral adductors increases with the growth of the shell, but the proportionate increase becomes less as the shells develop. Comparison of the height of the adductor platform with those of *S. preovalis* and its varieties, and *S. jukesi* var. *concava* reveals that it is proportionately greater, this increase in height being associated with the increase in the convexity of the ventral valve. The external proportions remain fairly constant throughout ontogeny and are similar to those of *S. preovalis*. The species has been found in the marine beds of the Collinsville district where it is represented by very large individuals in which the development of the adductor platform reaches an extreme, the anterior being raised into a high lip. The dorsal interior remains remarkably constant during ontogeny, the main changes being in the size and shape of the cardinal process and the thickening of the marginal ridges. The evolution of this species presents an interesting problem. The similarity between small individuals of this species and the large ones of *S. preovalis* (except in the case of teeth and dental callosities) is so marked that they might be regarded as variants of the one species, the former being a near descendant of the latter. However, comparison of representative groups of the two species does not confirm this deduction, and further, examination of *S. brittoni*, *S. clarkei*, and *S. clarkei* var. *minima* suggests that they may represent successive phases in the evolution of *S. ovalis*.

b. Occurrence. This species is common in the Springsure district where it characterises the Mantuan Downs *Productus* bed. It has been found in Parrot Creek (Collinsville district); in the Cracow district; and at several localities in the Serocold anticlimal structure (see map).

Range.—*S. ovalis* occurs only in the Mantuan Downs *Productus* bed and its equivalents, the age of which has never been determined. The age is probably late Kungurian.

EXPLANATION OF PLATE 57

FIGS. *1–3*—*Strophalosia jukesi* var. *concava* Maxwell, n. var. *1*, internal cast of ventral valve, UQ F15637, ×1, Wallaby Rocks, Stanthorpe. *2, 3*, holotype; internal cast of the ventral valve ventral view, ×1, and posterior view, ×2, UQ F15638, same locality. (p. 551)

4–14—*Strophalosia ovalis* Maxwell, n. sp. *4*, shell profile and outline; a = adductor scar, b = diductor scar. *5–7*, holotype; ventral, lateral and posterior views of internal cast of ventral valve ×1, UQ F15630, from 1½ miles NW of Consuelo Homestead, Springsure district. *8*, cardinal process, teeth and sockets, UQ F15632, ×3, from Sandy Creek, Rewan, Springsure district. *9*, cardinal process drawn from UQ F15635, ×6, from 2 miles E of Mantuan Downs Homestead. *10–12*, internal cast of ventral valve, lateral, posterior and ventral views, GSQ F1465, ×2, from 4½ miles up Parrot Creek, Bowen district. *13*, internal cast of ventral valve, UQ F15653, ×2, from 3 miles N of Mantuan Downs Homestead. *14*, dorsal view of shell, UQ F15631, from Fossil Ridge, 2.2 miles W of Cracow. (p. 548)

Abbreviations Used in the Explanations of Plates

UQ, University of Queensland, Dept. of Geology.
GSQ, Geological Survey of Queensland.
AM, Australian Museum, Sydney.
QM, Queensland Museum, Brisbane.
BMNH, British Museum (Natural History), London.

STROPHALOSIA JUKESI Etheridge, jr., 1880
Plate 56, figures 12–22

Strophalosia jukesi ETHERIDGE, JR., 1880, Proc. Royal Phys. Soc. Edinb., vol. 5, pp. 307–309, pl. 13, figs. 39–43.
Strophalosia jukesi ETHERIDGE, JR., 1884, Jour. Royal Soc. N.S.W., vol. 17, p. 88.
Strophalosia jukesi (Etheridge) PRENDERGAST 1943, Jour. Royal Soc. W. Australia, vol. 28, p. 47, pl. 5, figs. 18–20.

Holotype (here selected.—BMNH BB 9807, found in New South Wales and Tasmania; exact locality unknown; described and figured by Etheridge, 1880, figs. 39–40.

Remarks on types.—Two syntypes, BMNH BB9806, BB9808, were figured by Etheridge (1880, figs. 41–42). Etheridge based his original description on material in the Jukes collection from unknown localities in New South Wales, and on Davidson's collection from Tasmania. Examination of his types suggests that they belong to the species found in the Granton Quarry, Rathbone's Quarry and on the Huon Road 2 to 3 miles from Hobart, Tasmania.

Horizon.—*S. jukesi* has been found associated with a fauna equivalent to that of the Cattle Creek beds of Queensland. It occurs in the Cascades stage in Tasmania (Lewis, 1946).

Diagnosis.—Shell approximately equidimensional, subquadrate in outline. Hingeline narrow. Ventral valve moderately convex, sometimes weakly sinuate; dorsal valve weakly concave. Ventral area almost in the plane of the shell. Lateral walls of ventral valve steep. Ventral adductor platform low, of medium length. Dental callosities high, slightly bulbous or platelike. Thickening of the umbonal walls not marked.

Description.—External: The contour of the shell varies, but never becomes strongly convex ventrally or flat dorsally. Sometimes a weak sinus is developed although a median flattening is more common. The visceral cavity is never deep. In outline, the shell is slightly wider than high, and the hinge is narrow. The ventral umbo is weakly incurved over the cardinal area which rises at a low angle from the plane of the shell. Both valves carry lamellae and spines, the former being most abundant on the dorsal valve, the latter more numerous on the ventral valve.

Internal, ventral valve: The adductor muscle platform is low and of medium length. Diductor scars which are not sharply defined, occupy depressed subcircular areas. The remaining interior has a roughened surface resulting from the overlap of concentric growth lamellae and irregular vascular markings. Two small teeth project from the platelike dental callosities. The shell walls are not thickened to any marked degree, but they tend to rise steeply from a flat venter, giving the internal moulds of this valve a boxlike appearance.

Dorsal valve: The strong, bulbous cardinal process, supported by high cardinal ridges and median septum, is diagnostic of this species. The lateral lobes are weakly curved, but remain in contact with the central lobe of the process. The median septum which becomes narrower and higher anteriorly separates the two adductor scars, the latter occupying raised areas. Brachial ridges diverge from the junction of the anterior and posterior elements of the adductor scars. Thickening of the anterior and lateral margins has resulted in weak geniculation which is not reflected in the external contour.

Dimensions.—	Holotype (mm.)	Syntypes (mm.)		Other Specimens (mm.)	
Maximum width	35	37.0	34.5	27.0	38.6
Height, dorsal	30.0	35.0	31.5	24.5	33.0
Height, ventral	35.0	—	—	28.5	38.6
Hinge-width	18.0	21.0	18.5	—	24.0
Width/height, dorsal	1.17	1.06	1.11	1.10	1.17
Width/height, ventral	1.0	—	—	0.95	1.0
Width/hinge-width	1.94	1.76	1.87	—	1.60

Remarks.—a. Variation. In this species widest variation is found in the contour of the dorsal valve and in the outline of the shell. Variation in the length of the ventral adductor platform is associated with changes in the dorsal contour.

b. Related species. *S. jukesi* is readily distinguished from *S. clarkei* by the internal contour of the ventral valve, as well as external proportions. *S. jukesi* var. *concava* may also be distinguished by these characters. *S. typica*, which has been identified by some workers as *S. jukesi*, is distinguished by its strong, swollen dental callosities, deep ventral sinuation and different internal contour.

c. Correlations. This species has been found at three localities in Tasmania, in beds which belong to the Cascades stage, the latter having been equated with the Cat-

tle Creek beds and the earliest Cracow beds which are of Artinskian age.

STROPHALOSIA JUKESI var. CONCAVA Maxwell, n. var.

Plate 56, figures 23–24; Plate 57, figures 1–3

Strophalosia jukesi Etheridge, RICHARDS and BRYAN, 1924, Proc. Royal Soc. Queensland, vol. 34, pl. 20, fig. 4.

Holotype.—UQ F15638; found in the marine fossil horizon in the higher beds of the Wallaby Rocks, Stanthorpe Road fault block.

Diagnosis.—Strongly concavo-convex, non-sinuate shell; outline transversely oval to subcircular. Umbo strongly incurved, ventral area rising at a high angle from the plane of the shell. Hinge very narrow. Ornament strongly spinose, lamellose. Low, short ventral adductor platform. Dental callosities small. Septum and ridges strongly developed in the dorsal valve.

Description.—External: This variety is extremely concavo-convex, the greatest curvature being in the posterior region of the shell, and resulting in a strongly incurved umbo. In outline, the shell is subcircular and has a narrow hinge. A small umbonal cicatrix is usually developed. The ornament of both valves is strongly spinose and lamellose.

Internal, ventral valve: The adductor muscle platform is short and low, and is bordered by the adductor scars which occupy weakly depressed, striated areas on the valve floor. The remaining interior has a roughened surface resulting from the intersection of growth lamellae and depressions under the spine bases.

Dorsal valve: Characteristic of this valve is the strong cardinal process, buttressed by the two cardinal ridges and the median septum. It rises at an obtuse angle to the external surface and projects postero-ventrally. The lateral lobes are not curved and the central segment is divided into two elements by a median furrow. The attitude of the cardinal process changes during growth, the later deposition of shelly material tending to reduce the abruptness of its projection. The median septum is separated from the base of the cardinal process by a shallow depression. Cardinal ridges curve anterolaterally in a gentle arc from the base of the process. The adductor muscle scars occupy low elevations from which the brachial ridges diverge.

Dimensions.—	Holotype (mm.)	Topotypes (mm.)		
Maximum width	27.0	32.5	31.0	30.0
Height, dorsal	—	—	25.0	—
Height, ventral	23.0	28.5	—	25.0
Hinge-width	12.0	18.0	19.0	13.5
Length of ventral adductor scars	7.0	6.5	—	7.0
Overlap of ventral diductors	3.0	3.5	—	2.5
Distance of adductor scar from apex	4.5	7.0	—	6.0
Width/height, dorsal	—	—	1.24	—
Width/height, ventral	1.17	1.14	—	1.20
Width/hinge-width	2.25	1.80	1.63	2.22

Remarks.—The fauna of the Wallaby Rocks in which this variety is found was figured by Richards and Bryan (1924) and this form was identified as *S. jukesi.* It differs from the species sensu stricto in its outline, entire lack of sinuation, and in the contour of its valves. The age of the variety has not been determined as it has not been found associated with other fossils of known age. Its affinities with *S. jukesi* s.s. may suggest approximate age equivalence, i.e. Sakmarian-early Artinskian, but the solution of this problem will be found only when more faunas from the southern states have been investigated.

STROPHALOSIOID VARIATION AND ITS RELATION TO FUNCTION

Introduction

Variations in the characters of the genus *Strophalosia* are found to be closely related to the functions which each character performed. These variations and their functional relations are discussed in the following account. In the study of an animal, no organ nor function can be neglected however unimportant it may appear to be. Unless vestigial, each character has survived and evolved because, together with the other characters, it has withstood the rigorous screening of selection, animals with the most efficient organs being the most successful. The functions of all the organs are so coordinated as to provide maximum efficiency in the life processes of the animal, and varia-

tion in one will result in corresponding adjustments in the others, thus preserving the functional stability of the animal as a whole. In the protremate brachiopods, three at least, of the factors on which survival depended, were strongly influenced by articulation. It is the variation in the organs controlling articulation with which we are concerned. Although fossil evidence is invariably incomplete, variations in characters controlling one function will be reflected by corresponding changes in the others, and it is by the integration of such evidence that the complete development of the animal can be deduced.

Articulation

For at least part of its life, *Strophalosia* was maintained in a vertical or oblique position by umbonal cementation. Since gravity becomes an important factor as the valve departs from the vertical, it is essential to consider "shell attitude" when analysing the functions of various characters. The position and plane of the umbonal cicatrix of *Strophalosia* suggest that the normal shell attitude was similar to that illustrated diagrammatically in figure 2, i.e. oblique.

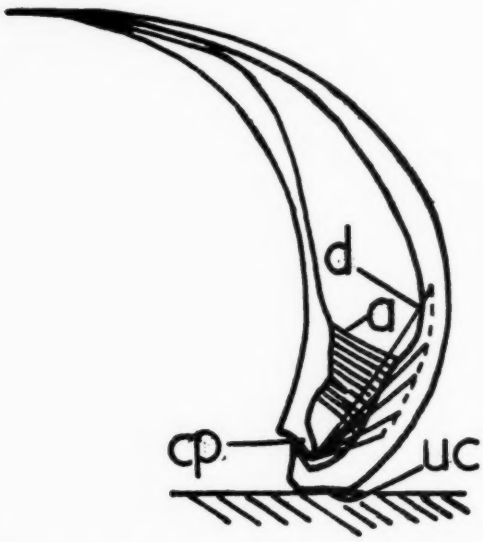


FIG. 2.—Longitudinal section through the median part of the shell illustrating its attitude during life. cp = cardinal process, uc = umbonal cicatrix, d = diductor muscle, a = adductor muscle.

From figure 2 it is obvious that greater forces are involved in the closing of the valves than in shell opening, since in the former case the movement is against gravity, and in the latter, with gravity. In the case of *Strophalosia*, variation associated with the adductor system is the more obvious, and it is this system which will now be considered.

Adductor muscles.—These are components of a simple lever system. The ventral adductor muscle platforms show wide variation, not in relative positions as is the case with the diductor scars, but in their height and length. This variation is closely related to the variation in the shell contour. Consider the closing mechansim of the concavo-convex shell in an oblique position (see fig. 3). When the anterior point of muscle attachment is fixed, the maximum moment is determined by joining that point to the fulcrum and projecting the perpendicular from the line at this point (fig. 3A). In strongly concave dorsal valves this perpendicular will be directed more posteriorly than in the less concave valves (fig. 3B). Consequently, the adductor muscle platform in the ventral valve extends further anteriorly when the dorsal valve tends towards flatness and vice versa.

The other variation in the type of muscle platform is controlled by the convexity of the ventral valve. The surface of attachment, if perpendicular to the direction of the muscle force, will permit higher efficiency in the adductor system, than when the surface is oblique to this direction. This results in the raising of the anterior part of the platform, particularly in the strongly convex valves. In addition, raising of the platform decreases the distance between the area of muscle attachment on the two valves, thus permitting a larger visceral cavity without necessitating increased length of muscle. In less convex ventral valves the surface of attachment remains more or less parallel with the curvature of the valve floor, for reasons similar to those above.

In summary, it may be stated that the height of the ventral adductor platform varies directly with the convexity of that valve, its length varying inversely with the concavity of the dorsal valve. In the Queensland species of *Strophalosia* these relations

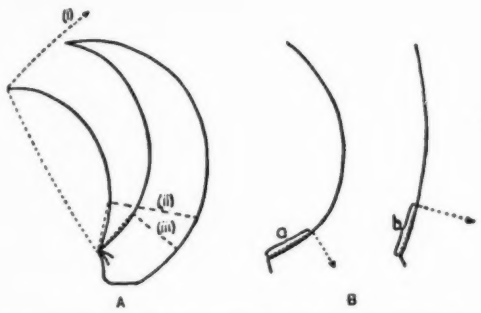


FIG. 3—A. Median longitudinal section through shell illustrating (i) theoretical directions for maximum moment, (ii) direction of force exerted by adductor when shell is open, and (iii) when closed.

B. Sections of strongly concave and weakly concave dorsal valves showing relative directions of forces producing the maximum moment possible for the adductors. Distances a and b are equal. Note the wide difference in the directions of the muscle forces.

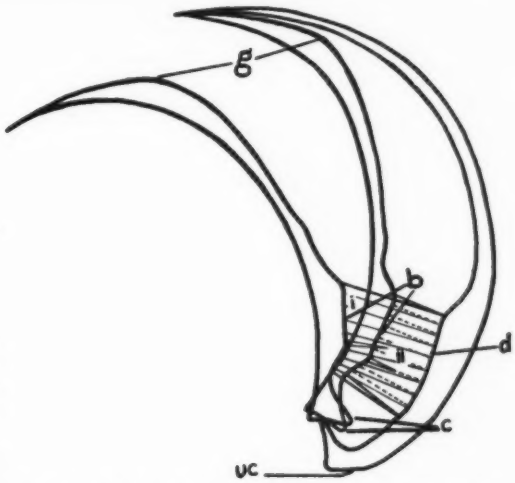


FIG. 4—Median longitudinal section through the shell, showing the attitude of the adductor muscles for (i) open and (ii) closed shell. g = geniculation, b = adductor scar, c = cardinal process, uc = cicatrix, d = ventral adductor scar.

are clearly illustrated, and we have the following groups:

i. Adductor platform high, medium length. Ventral valve moderately convex. Dorsal valve moderately concave; e.g. *S. ovalis, S. brittoni.*

ii. Adductor platform low, short. Ventral valve moderately convex. Dorsal valve strongly concave; e.g. *S. preovalis, S. jukesi* var. *concava.*

iii. Adductor platform low, long. Ventral valve moderately convex. Dorsal valve weakly concave to flat; e.g. *S. typica, S. clarkei, S. jukesi.*

The final variation to be considered is in the dorsal adductor muscle scars, which are divided into posterior and anterior elements. The former slope more steeply posteriorly than the anterior elements. The purpose of such division is not obvious, but it may be the result of the articulatory process. Thus, when the valves are open, muscular control is directed on the posterior element to effect closure, and when closed, the valves are held in that position by forces concentrated on the anterior element (see fig. 4). Little variation is found in the shape of these scars, although the height and slopes of the elevations do vary.

Diductor muscles and the cardinal process.—Shell opening is effected by a simple first order lever system as shown in figure 5A. The muscle is attached to the dorsal face of the cardinal process, but the process still behaves as a first order lever.

For maximum mechanical efficiency, the direction of force is perpendicular to the lever. Should the direction not be perpendicular, the moment is decreased. In figure 5C, BF represents the ideal direction; when BF′ is used the efficiency is reduced, since the moment BF′ · CA is less than BF · AB. Therefore, for greatest mechanical advantage, the muscles should be capable of directing their force as shown. Shell shape, attitude of the cardinal process and the size of the valves

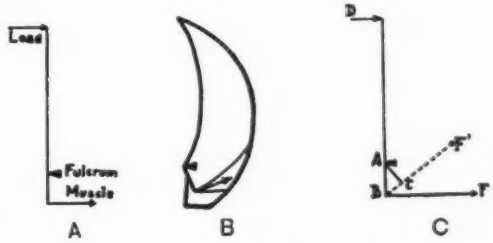


FIG. 5—A. Lever system of *Strophalosia.* B. Section showing position of the muscles and cardinal process. C. Diagram showing directions of force necessary for the maximum moment, viz: BF (see text)

determine the position of the muscles and hence their efficiency. The number of variables involved renders a study of the diductor system very complex. In *Strophalosia* slight variations in the position of the ventral diductor scars have been found.

Several other combinations of valve shapes are possible, but the unwieldy muscle systems required for their articulation do not warrant consideration. Due to the poor definition of the anterior margin of the ventral diductor muscle scars, it is difficult to obtain the dimensions necessary for the comparison of different species, and the value of these scars as specific criteria is therefore negligible. In addition, wide variation in their position is found, due probably to the fact that several variables are involved in the determination of their position.

Dental callosities and teeth.—Variation in the size of these is of value in specific differentiation. Their development is strongest in shells with high delthyrial cavities, e.g. *S. brittoni*, *S. typica* and to a lesser extent *S. clarkei*. It is significant that these species are characterised by slightly concave dorsal valves and moderately convex ventral valves, whereas strongly concavo-convex species such as *S. preovalis* and *S. ovalis* have very small dental callosities. In *S. jukesi* the callosities are intermediate in size between those of the two previous groups. The function of these structures is not apparent, but it seems that the manner of their development is closely related to the shape of the shell. Dental callosities and shell contour are the two most useful criteria for the recognition of species.

Median septum, brachial ridges and cardinal ridges.—These structures, although involved in the process of articulation, show little variation within the genus. One might infer then, that the possible range of variation in these structures for strophalosioid articulation is small, and as specific criteria they are valueless. However, the differences in articulation between different genera (or families) have been sufficient to reflect differences in these characters. The only intrageneric variation is found in the size of these structures, e.g. in certain individuals of *S. clarkei* where there is abnormal development of shell substance in the dorsal valve, these structures are large. In individuals of *S. preovalis* where the shells are more fragile, these structures are less prominent.

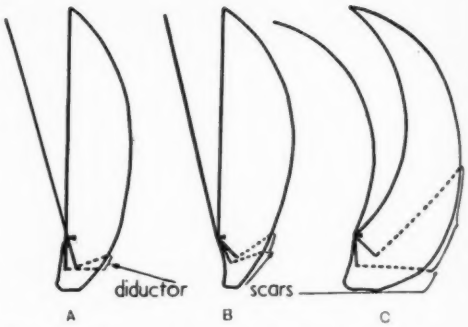


FIG. 6—Three median longitudinal sections illustrating the different shell profiles and their related diductor systems. A. Flat dorsal valve, weakly convex ventral valve, incurved umbo. In this case the cardinal process can project in the same plane as the dorsal valve, and for the maximum moment, the muscle is attached to the ventral valve as shown. The anterior margin of the scar is influenced by the direction of the muscle force when the shell is open. If the posterior region of the ventral valve is approximately parallel to the plane of the cardinal process, the muscle scar is short. As it departs from this parallelism (i.e. becomes more curved) the length of the scar increases. In *Strophalosia* short scars are common, as the ventral posterior region is usually strongly curved.

B. Flat or weakly concave dorsal valve, weakly convex ventral valve; umbo not incurved. Cardinal process projects posteroventrally and the ventral muscle scars are situated farther anteriorly and are longer than those in the previous example.

C. Concave dorsal valve, strongly convex ventral valve, incurved umbo. The muscle scars tend to be long.

Shell Contour

Sutton (1938) and Fredericks (1915) based their major subdivisions of the Productacea on shell shape, but investigation of *Strophalosia* has shown that its species and varieties may vary in shape from planoconvex to extremely concavo-convex. Geniculation is another character which shows considerable variation within the genus, the degree of geniculation changing at successive stages of ontogenetic development. The degrees of ventral convexity, dorsal concavity and ventral sinuation provide useful criteria for the specific differentiation of this genus, and when combined with dental callosities, these characters may be used in

determining the phylogenetic development of the group. The main types of shell contour which can be distinguished are as follows:

i. Ventral valve strongly convex; nonsinuate; umbo incurved; dorsal valve moderately concave, e.g. *S. ovalis*.

ii. Ventral valve moderately convex, nonsinuate or weakly sinuate; umbo incurved; dorsal valve flat to weakly concave, e.g. *S. brittoni*, *S. clarkei* and *S. jukesi*.

iii. Ventral valve weakly convex, sinuate; dorsal valve flat, e.g. *S. typica*.

iv. Ventral valve strongly incurved posteriorly, non-sinuate, e.g. *S. jukesi* var. *concava*.

In all four types a trail and geniculation are developed, the degree of their development varying with the different species, but they are most prominent in the first group. Geniculation results from the anterior thickening of the dorsal valve, as shown in figure 7A. In certain forms of *S. clarkei* this thickening reaches an extreme, and a strong ridge or diaphragm is developed (see fig. 7B).

Forms which do not develop long trails usually have large cicatrices. Thus the development of the trail may be associated with a change in the attitude of the shell during life, those forms with long trails becoming unattached at some stage of their ontogeny.

Shell Outline

Measurement of the height and width of the shell and of the width of the hinge has shown that variation within the species is almost as wide as that between these groups. No progressive change is found in the width-height ratio of the shell during ontogeny. External proportions are of little value as specific criteria.

PHYLOGENETIC CHANGES

In the eastern Australian species of *Strophalosia* two plexi can be recognised, these being the "*preovalis-clarkei-ovalis*" and the "*jukesi*" groups. The former is more abundant in Queensland. The stratigraphical distribution of the members of these plexi is illustrated in Table 3.

The "*preovalis-clarkei-ovalis*" Plexus

The earliest members of this group are found in the Dilly fauna, viz. *S. preovalis* var. *pristina*, which is a very small form. The species *S. preovalis* and *S. brittoni* occur in the succeeding faunas of the Cattle Creek beds and their equivalents. Except for increased size, *S. preovalis* showed little change from the earlier stock, whereas *S. brittoni* began to evolve rapidly. The trends were towards larger size, steeper walls, higher delthyrial cavity and large dental callosities. Weak sinuation also developed. These trends reached a maximum in the latest members of the Homevale-Blenheim fauna (i.e., Cattle Creek equivalent), but in the early fauna of the Big *Strophalosia* bed (i.e., Ingelara equivalent), the size of the dental callosities, delthyrial cavity and sinuation had decreased considerably. *S. brittoni* var. *gattoni* reflects this regression of characters. At this stage two other species diverged, *S. typica* and *S. clarkei*. In the former the trends towards sinuation and large dental callosities were maintained, but the convexity of the ventral valve and the concavity of the dorsal valve decreased, with resultant changes in the ventral adductor platform. Neither *S. brittoni* nor *S. typica* survived the early part of the Big *Strophalosia* bed. *S. clarkei*, apparently the most vigorous of all the species so far evolved, continued the trend towards plano-convexity, loss of sinuation, loss of

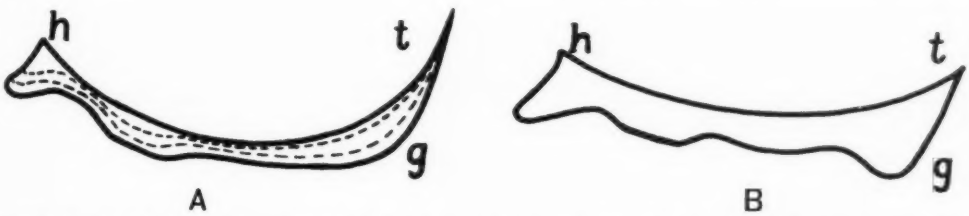


FIG. 7—Profile of the dorsal valve. A. Normal geniculation, with the dotted lines indicating successive stages of growth. B. Section showing abnormal thickening in some forms of *S. clarkei*. h = hinge, g = geniculation, t = trail.

TABLE 3—STRATIGRAPHICAL DISTRIBUTION OF THE SPECIES OF *Strophalosia* IN EASTERN AUSTRALIA

Stratigraphic Sequence	Evolutionary Sequence
Mantuan *Productus* bed	*S. ovalis*
Catherine sandstone	*S. clarkei* var. *minima*
Ingelara beds	*S. typica* *S. brittoni* var. *gattoni* *S. clarkei*
Aldebaran sandstone	*S. jukesi* var. *concava*
Cattle Ck. beds	*S. preovalis* *S. brittoni* *S. jukesi*
Staircase sandstone	
Dilly beds	*S. preovalis* var. *pristina*

umbonal thickening and smaller dental callosities. This species survived Ingelara times, but it began to show wide variation. Some individuals developed plano-convex shells with extremely thickened dorsal valves, others became very large, while a group of small, concavo-convex, weakly sinuate shells also evolved. All are characteristic of the upper part of the Big *Strophalosia* bed, and the last group has been separated as *S. clarkei* var. *minima*. It appears to be the forerunner of *S. ovalis* in which sinuation or medial flattening disappeared, dental callosities decreased and umbonal thickening developed still further. The characters of *S. ovalis* closely resemble many of those of *S. preovalis*. Thus the evolution of this plexus may be summarised as an initial divergence from, and then a gradual regression towards "preovalian" characters. The changes in shell profile and umbonal structure are represented in figure 8.

The "*jukesi*" Plexus

S. jukesi, which is characteristic of the Cascades stage of Tasmania, is similar to *S. gerardi*, and it may have been derived from stock which migrated from the Indian province. Absence of the species s.s. from the Queensland faunas suggests that some barrier, geographic, climatic or ecological, separated the northern and southern provinces of Australia during early Permian times. Although *S. jukesi* var. *concava* is related to the the Tasmanian species, it has not been possible to determine the nature of this relation, i.e. whether ancestral, descendant or contemporary. No descendants appear to have evolved in Queensland during the Permian.

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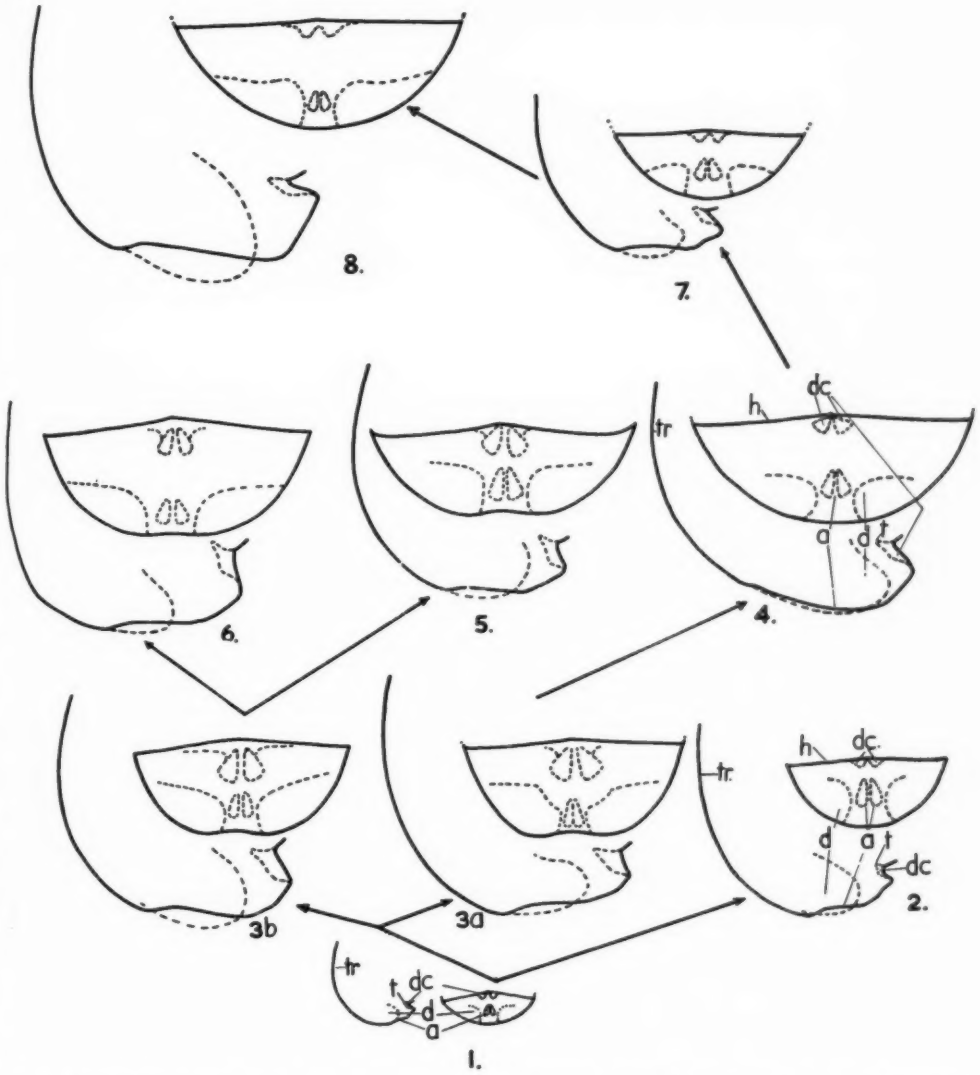

FIG. 8—Longitudinal profiles and transverse sections of internal casts of the species in the "*preovalis-clarkei-ovalis*" plexus. The longitudinal profiles are drawn through the median part of the shell, the dotted lines indicating the structures lateral to this plane. The transverse sections are drawn through the widest part of the venter, just anterior to the adductor muscle platform. They show the contour of the shell (whether sinuate or non-sinuate), and the relative position and size of the structures posterior to the section are indicated by the dotted lines. h = hinge, dc = dental callosity, t = teeth, tr = trail, d = diductor scar, a = adductor scar.

The species are arranged in phylogenetic sequence, the arrows indicating the directions in which they evolved. 1, *S. preovalis* var. *pristina;* 2, *S. preovalis;* 3, *S. brittoni* (a, forerunner of *S. typica,* b, forerunner of *S. brittoni* var. *gattoni*); 4, *S. clarkei;* 5, *S. typica;* 6, *S. brittoni* var. *gattoni;* 7, *S. clarkei* var. *minima;* 8, *S. ovalis.* Marked changes in successive species are seen in the height and size of the dental callosities, the contour of the umbonal region and the sinuate or non-sinuate nature of the venter.

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POSTSCRIPT NOTES OF THE OSTRACODE *TRACHYLEBERIS*

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ABSTRACT—Certain previously published figures of the hinge of *Trachyleberis* are criticised. The authors correct their previously published synonymy of the type species and clarify the nature of the type specimens. Validly proposed names for genera thought to be closely related to *Trachyleberis* are listed. The spelling of the family and subfamily names based on the genus is corrected to Trachyleberididae and Trachyleberidinae, respectively, in accordance with the new requirements of the Rules of Nomenclature.

Hinge Structure.—In a recent paper (Harding and Sylvester-Bradley, 1953) we have refigured the type species of *Trachyleberis*, *T. scabrocuneata* (Brady). Dr. I. G. Sohn has pointed out to us (personal communication) that in former figures of this species (Sylvester-Bradley, 1948, pl. 122, fig. 18 and text-fig. 1c) the posterior tooth of the right valve is set at an angle to the median element, whereas in our new figures it is shown as parallel to the median element. We have re-examined the specimen from which the 1948 figures were drawn, and find that the drawings were inaccurate in this feature. Plate 2, figure 10 and text-figure 3 of our 1953 paper are correct.

Synonymy.—Dr. Stuart Levinson has drawn our attention (personal communication) to an inaccuracy in the synonymy of *T. scabrocuneata* in our joint paper (1953) given on p. 11. The first two lines of this synonymy (which refer to Brady, 1880) should be corrected to read as follows:

Cythere scabrocuneata BRADY, 1880, Challenger Rept. 1: p. 103 (part); pl. 17, figs. 5 e, f; ? pl. 17, figs. 5 a–d; *not* pl. 23, figs. 2 a–c.

Paratypes.—Puri (1953a) has published a paper on *Trachyleberis* which appeared shortly before ours. In it he suggests that the "paratypes" figured by Sylvester-Bradley, 1948 (and some of which we refigure in our 1953 paper) are not the specimens used by Brady, the original author, in 1880. In this, Puri is mistaken. The specimens are those used by Brady in 1880. As, however, the term "paratype" has not, perhaps, a generally accepted definition, we would like to make it clear now that we have used the term in the sense of Calman (1949, p. 30) as: "the remainder of the syntypes" after the selection of a lectotype. It is true that, as Puri has pointed out, the size given by Brady for the female is 0.77 mm., whereas that figured by Sylvester-Bradley, 1948, is 0.91 mm. (not 1.10 mm., as given by Puri; that is the size of the male carapace). This discrepancy may be due either to inaccuracies in Brady's measurements, or to the fact that this measurements may apply to one of the other syntypes from a different locality which are now lost.

We might, perhaps, here mention that the lectotype is a male on two slides (1952.12.10. 1 and 2), one holding the two valves of the shell and the other containing some dissected parts: the right and left penes and a few appendages.

Taxonomy.—The taxonomic position of *Trachyleberis* is still one of uncertainty and difference of opinion. We feel it would be a help to paleontologists generally if we here list (Table 1), in order of priority, the genera that we believe to be more or less closely allied to *Trachyleberis*. Some of these genera we believe to be synonyms of each other. The type species of *Archicythereis*, *Buntonia Puriana* and (probably) *Anticythereis* are based on immature specimens, but the names have validity, and cannot be disposed of unless officially classed as nomina dubia.

Subfamily names.—We consider the subfamily "Cythereiinae" Berousek, 1952 (type genus *Cythereis*) to be synonymous with Trachyleberinae Sylvester-Bradley, 1948. The name of the subfamily based on *Cythereis* should, we believe, correctly be spelt "Cythereidinae" (see Hemming, 1953, p. 34). For the same reasons, (according to the new directives given at Copenhagen revising the Paris decisions referring to the formation of family names) the family and subfamily based on *Trachyleberis* should in

TABLE 1—GENERA CLOSELY ALLIED TO *Trachyleberis*

Genus:	Type-species:	Type-horizon:
Cythereis Jones, 1850	*Cytherina ciliata* Reuss, 1845	L. Cretaceous
Trachyleberis Brady, 1898	*Cythere scabrocuneata* Brady, 1880	Recent
Pterygocythereis Blake, 1933	*Cythereis jonesii* Baird, 1850	Recent
Buntonia Howe, 1935	*B. shubutaensis* Howe, 1935	Eocene
Archicythereis Howe, 1936	*Cythereis yazooensis* Howe & Chambers, 1935	Eocene
Pyricythereis Howe, 1936	*Cythereis? israelskyi* Howe & Pyeatt, 1935	Eocene
Isocythereis Triebel, 1940	*I. fissicostis* Triebel, 1940	L. Cretaceous
Platycythereis Triebel, 1940	*Cythereis excavata* Chapman & Sherborn, 1893	U. Cretaceous
Anticythereis van den Bold, 1946	*Pseudocythereis reticulata* Jennings, 1936	U. Cretaceous
Oligocythereis Sylvester-Bradley, 1948	*Cythereis fullonica* Jones & Sherborn, 1888	M. Jurassic
Occultocythereis Howe, 1951	*O. delumbata* Howe, 1951	Eocene
Hirsutocythere Howe 1951	*H. hornotina* Howe, 1951	Eocene
Bradleya Hornibrook, 1952	*Cythere arata* Brady, 1880	Recent
Quadracythere Hornibrook, 1952	*Cythere truncula* Brady, 1880	Recent
Rectotrachyleberis Ruggieri, 1952	*Cythereis hamata* G. W. Müller, 1894	Recent
Actinocythereis Puri, 1953 a	*Cythere exanthemata* Ulrich & Bassler, 1904	Miocene
Puriana Coryell & Fields, 1953	*Favella puella* Coryell & Fields, 1937	Miocene
Trachyleberidea Bowen, 1953	*Cytheris prestwickiana* Jones & Sherborn, 1887	Eocene

future be known as Trachyleberididae and Trachyleberidinae respectively (Greek *leberis*, genitive *leberidos*, a shell).

Acknowledgments.—We should like to thank Drs. Levinson and Sohn for their courtesy in drawing our attention to the first two points discussed in this note.

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QUANTITATIVE STUDIES OF BRACHIOPODS FROM THE LOWER CARBONIFEROUS REEF LIMESTONES OF ENGLAND
II. *PUGNAX PUGNUS* (MARTIN) AND *P. PSEUDOPUGNUS* N. SP.

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ABSTRACT—Four collections of *P. pugnus* and two of *P. pseudopugnus* n. sp. are compared, all from the *Dibunophyllum* zone. Both species exhibit much variation in shape and the assemblages of *P. pugnus* differ significantly from each other in certain respects. Insufficient evidence is available for a similar conclusion to be drawn from *P. pseudopugnus*, but the limited information available suggests that the latter species may be more uniform than the former. Both species display allometric growth of length in relation to width. Relative growth of thickness and width is approximately allometric.

INTRODUCTION

This paper summarises a detailed biometrical investigation of 2,245 specimens of *Pugnax*, either belonging to, or resembling, the group of *P. pugnus* from the *Dibunophyllum* zone of the Lower Carboniferous of England. It is considered that two species only are represented: *P. pugnus* (Martin) and *P. pseudopugnus* n. sp. Four out of the six collections studied are from reef limestone exposures near Castleton, Derbyshire, and are precisely localised. The other two are composite samples from the Craven Reef Belt, Yorkshire, which forms part of the Tiddeman Collection in Skipton Museum. Martin's type of *P. pugnus* has also been examined.

The following characters of the shell have been considered; (1) length, (2) width (breadth), (3) thickness, (4) depth, (5) number of costae on median fold of brachial valve, (6) total member of costae on brachial valve. The terms length, width and thickness are those conventionally used for brachiopods. The depth (B. Simpson, 1933) is the sum of the thickness (which is measured through the middle of the shell) and the depth of the sulcus (Fig. 1).

Acknowledgments.—I wish to thank Mr. C. H. Leigh-Dugmore for invaluable help and advice on statistical procedures and for checking (and occasionally correcting) many of my computations. Thanks are also due to Mr. B. J. A. Martin for helpful suggestions and criticism and to Mrs. P. E. Pritchard who, in the early stages of the work, carried out many and varied analyses. The photography is the work of Mr. H. R. Willcocks who has also drawn the diagrams from my rough copies, except Figures 1 and 12 which were drawn by Mr. T. E. H. Gray. I am indebted to Mr. B. Simpson for the loan of specimens from Swansea University College and to Dr. A. Raistrick and Mr. A. Dunn for the loan of specimens from the Tiddeman Collection in Skipton Museum.

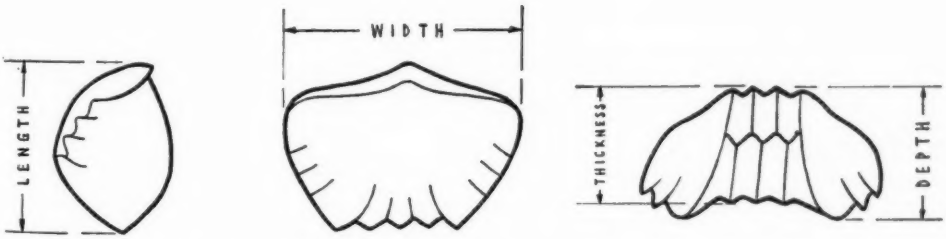

FIG. 1—Diagrammatic representation of the dimensions of *Pugnax pugnus*.

DESCRIPTION OF *Pugnax pugnus* (MARTIN)

The shell is rhynchonelliform with a broad sulcus in the pedicle valve and a corresponding fold in the brachial valve. The plications and costae are acute and rounded or sub-angular, the costae not extending to the posterior parts of the valves. There are from two to eight centre plications on the brachial valve with one fewer on the pedicle valve and from one to five plications on each flank. A median incision is seen in the costae of well-preserved specimens, particularly near the anterior margin of the sinus of the pedicle valve. This feature is present in the holotype (re-figured Muir-Wood, 1951, Pl. 4) and is discernible in some of the specimens illustrated here (Pl. 58). The anterior margin is sometimes simple, but is more usually divided into two or more layers.

The internal characters are as shown in Weller (1914). There is no median septum in the brachial valve, but some specimens show a faint median line suggestive of a septum. This, however, always disappears when the surface layer is removed by grinding or solution.

CAVE DALE COMMUNITY

A collection of 600 specimens of *Pugnax* from the *pugnus* bed of Cave Dale, Castleton (Parkinson 1947), was examined by B. Simpson (1933) who suggested that two species were represented, *Pugnax pugnus* (Martin) and *P.* cf. *P. sulcatus* (J. de C. Sowerby). This collection, which is deposited in Swansea University College, has kindly been lent to the author by Mr. Simpson.

Simpson's conclusion that the Cave Dale community consists of two species was based in the first place on suggestions of bimodality in three of the four frequency polygons of the ratios of dimensions. He found in general that the specimens falling within the areas enclosing the two peaks differed in the nature of the anterior magin and in the sharpness of the costae and plications. He noticed that the forms resembling the holotype in having a layered anterior margin usually fell within the area enclosed by the larger peak. The generally less inflated forms with the simple margin he separated under the name of *Pugnax* cf. *P. sulcatus* (J. de C. Sowerby). Plate 58 of the present paper illustrates specimens with both types of margin.

When the Cave Dale sample is subdivided according to the nature of the anterior margin as was done by Simpson, significant differences are found between the two groups. Nevertheless the writer believes, for the following reasons, that one species only is present:

1. There is no sharp distinction between the specimens with a simple anterior margin and those with a layered margin. The plicated margin of occasional specimens has in fact only bifurcated into two or three layers over part of its length. (Where more than three layers are present they are usually obscure and difficult to recognise individually. As many as six are apparently present in some specimens.)
2. The frequency polygons drawn by Simpson are thought to be too irregular in outline to justify the assumption of bimodality.
3. The proportions of the "layered" and "unlayered" specimens from two other areas, Treak Cliff and the Craven Reef Belt, are of the same order (about $3\frac{1}{2}$ to 1) as those from Cave Dale. A χ^2 test (see text books on statistics) shows no significant differences between the three samples in this respect. If two species are present it would be an unusual coincidence for their proportions to be so similar in the three assemblages.

Simpson's suggestion that the form with the unlayered anterior margin (the "thin" form) should be referred to *Pugnax* cf. *P. sulcatus* was based on an illustration (Parkinson, 1926) of an unusual form showing resemblance to J. de C. Sowerby's type, which is a variety of *P. acuminatus* and is readily distinguished from *P. pugnus* by the absence of plications and costae on the flanks.

COMPARISON OF THE COLLECTIONS

The sample of 829 specimens from Cave Dale comprises 216 specimens collected by the writer, 19 specimens from the Birmingham University collection presented by J. Wilfrid Jackson and the rest from the Swan-

TABLE 1.—COSTAE ON MEDIAN FOLD ON BRACHIAL VALVE

Number of Costae	Number of Specimens			Mean Number of Costae	
	Cave Dale	Treak Cliff	Craven Reef Belt		
2	4	1	0	Cave Dale	4.120
3	155	6	22		
4	412	23	77	Treak Cliff	4.633
5	229	40	170		
6	16	9	120	Craven Reef	5.221
7			38		
8			7		
	816	79	434		

Significance of differences between collections.

	χ^2	Degrees of freedom
Cave Dale and Treak Cliff	46.44	3
Cave Dale and Craven Reef	383.77	3
Treak Cliff and Craven Reef	22.26	3

TOTAL COSTAE ON BRACHIAL VALVE

Number of Costae	Number of Specimens			Mean number of Costae	
	Cave Dale	Treak Cliff	Craven Reef Belt		
3	8		2	Cave Dale	8.788
4	14		2	Treak Cliff	9.478
5	23		6	Craven Reef	10.475
6	19	1	4		
7	65	6	9		
8	164	10	27		
9	145	17	41		
10	131	16	58		
11	83	11	79		
12	24	5	43		
13	9	1	33		
14	2		29		
15			17		
16			7		
17			3		
	687	67	360		

Significance of differences between collections.

	χ^2	Degrees of freedom
Cave Dale and Treak Cliff	8.32 (not significant)	5
Cave Dale and Craven Reef	247.16	7
Treak Cliff and Craven Reef	29.26	5

sea University College collection. It comes from a deposit about five feet thick and a few feet in lateral extent in D1 reef limestone which has yielded a varied fauna to Dr. Jackson, including the goniatite *Beyrichoceras castletonense* Bisat.

The Treak Cliff (near Castleton) assemblage consists of 83 specimens collected by the author from a thickness of about 50 feet in upper D1 reef limestone.

Four further specimens from the Castleton area included in the study were obtained from the reef limestone of Mich Low, near Bradwell, which is considered to be of lower D2 age (Parkinson, 1947).

The sample of 434 specimens from the Craven Reef Belt, Yorkshire (D1—lower D2), was separated from a large number of rhynchonellids which includes many hundreds of specimens of the species described in this paper as *Pugnax pseudopugnus*.

Several methods of analysis have been employed, of which three are considered here: (1) the Chi Square test to compare the number of costae, (2) comparison of means and variances of ratios, (3) Kermack and

TABLE 2.—STATISTICS OF CHARACTERS

L = length; W = width; T = thickness; D = depth. C_M = number of costae on median fold of brachial valve; C_T = total number of costae (including those on the flanks) of brachial valve; N = number of specimens. All dimensions are in millimetres.

Locality	Character	N	Range	Mean	Standard Deviation
Cave Dale	W	829	9.1 –34	19.41	3.698
	L	829	7.8 –23.5	15.24	2.653
	T	829	3.2 –17.9	9.86	2.950
	D	828	3.2 –19.1	10.91	3.450
	L/W	829	0.54 – 1.00	0.7884	0.0506
	T/W	829	0.28 – 0.75	0.5024	0.0890
	D/W	828	0.28 – 0.86	0.5539	0.1086
	C_M/W	816	0.09 – 0.44	0.2151	0.0459
	C_T/W	687	0.18 – 0.73	0.4519	0.0800
Treak Cliff	W	83	10.4 –28.2	19.60	3.362
	L	83	9.1 –24.3	15.68	2.684
	T	83	3.6 –17.8	10.21	2.783
	D	83	3.6 –17.9	11.75	3.290
	L/W	83	0.64 – 0.95	0.8015	0.0627
	T/W	83	0.30 – 0.66	0.5157	0.0903
	D/W	83	0.30 – 0.76	0.5883	0.1078
	C_M/W	79	0.10 – 0.35	0.2340	0.0497
	C_T/W	67	0.34 – 0.85	0.4814	0.0818
Craven Reef Belt	W	434	10.2 –36.2	22.72	3.703
	L	434	9.5 –27.4	18.09	3.368
	T	434	4.5 –20.8	12.53	1.610
	D	434	4.5 –20.5	14.23	3.100
	L/W	434	0.64 – 1.00	0.8043	0.0523
	T/W	434	0.32 – 0.71	0.5522	0.0712
	C_M/W	434	0.10 – 0.42	0.2337	0.0496
	C_T/W	359	0.19 – 0.98	0.4837	0.0990
Mich Low	W	4	27.6 –35.1	30.82	3.148
	L	4	22.4 –25.8	24.55	1.588
	T	4	15.7 –21.1	17.97	2.259
	D	4	17.7 –24.3	19.90	3.050
	L/W	4	0.735– 0.835	0.7992	0.0441
	T/W	4	0.446– 0.685	0.5887	0.1028
	D/W	4	0.512– 0.788	0.6492	0.1129

Haldane's reduced major axis as an estimate of linear relationships (1950).

The first of these techniques constitutes a relatively rapid method of testing whether two samples are likely to be drawn from the same or from different populations. It is seen in Table 1 that the average number of costae is greater at Treak Cliff than in Cave Dale and greater still in the Craven Reef Belt. The Chi Square test shows that in five of the six comparisons the differences are highly significant. Except in the comparison between Treak Cliff and Craven the differences are greater than can be accounted for by differences in width of the shell. As would be expected costation tends to increase with shell width.

To illustrate the second method of comparison a list of the different statistics is given in Table 2 and histograms of certain of the distributions are drawn in Figures 2, 3 and 4. The results of the tests of significance are given in Table 3.

The third method compares the coefficients and intercepts of the Kermack and Haldane lines for length-width and thickness-width (Tables 4 and 5). Significant differences are found in the T-W relation between Cave Dale and Craven Reef and between Treak Cliff and Craven Reef.

Summing up we find that the analyses show significant differences in some respects between all the samples, but there is less difference between the Cave Dale and Treak Cliff samples than between those from Cave Dale and the Craven Reef. The latter as-

TABLE 3.—SIGNIFICANCE OF DIFFERENCES BETWEEN RATIOS
S = significant at one per cent level of probability.
N.S. = not significant.

	Ratio	Means		Variance Ratios	
Cave Dale and Treak Cliff	L/W	t = 2.18	N.S.	F = 1.34	N.S.
	T/W	t = 1.25	N.S.	F = 1.03	N.S.
	D/W	t = 2.75	S.	F = 1.03	N.S.
	C_M/W	t = 3.56	S.	F = 1.17	N.S.
	C_T/W	t = 2.88	S.	F = 1.04	N.S.
Cave Dale and Craven Reef	L/W	t = 4.51	S.	F = 1.07	N.S.
	T/W	t = 10.82	S.	F = 1.56	S.
	C_M/W	t = 5.81	S.	F = 1.17	N.S.
	C_T/W	t = 5.26	S.	F = 1.53	S.
Treak Cliff Craven Reef	L/W	t = 0.51	N.S.	F = 1.42	N.S.
	T/W	t = 3.48	S.	F = 1.60	S.
	C_M/W	t = 0.015	N.S.	F = 1	N.S.
	C_T/W	t = 0.18	N.S.	F = 1.47	N.S.

semblage is drawn from a bigger area and probably a greater stratigraphical range than that from Treak Cliff. In most of its characters the Treak Cliff form does not differ significantly from the Cave Dale form, but it has a significantly greater number of costae. This is not a consequence of greater size as there is no appreciable difference between the mean shell widths at the two localities. The Treak Cliff horizon is thought to be higher than the *pugnus* bed of Cave Dale (Parkinson, 1947), but there is not enough evidence to state that the difference in costation is a consequence of a difference in stratigraphical level. The four specimens from Mich Low (D2) are all large ones and most of the characters show apparent significant differences from Cave Dale, but it would be unwise to draw conclusions from so small a sample as the randomness is open to question.

TABLE 4.—EQUATIONS EXPRESSING RELATIONS BETWEEN THE DIMENSIONS

L = length W = width T = thickness

Cave Dale

$L = 1.021\ W^{0.912}$ Log L = 0.912 log W + 0.009
$T = 0.097\ W^{1.554}$ Log T = 1.554 log W − 1.014

Treak Cliff

$L = 0.847\ W^{0.981}$ Log L = 0.981 log W − 0.722
$T = 0.097\ W^{1.563}$ Log T = 1.563 log W − 1.014

Craven Reef Belt

$L = 0.023\ W^{0.955}$ Log L = 0.955 log W − 0.035
$T = 0.234\ W^{1.273}$ Log T = 1.273 log W − 0.631

The holotype of *P. pugnus* (Sowerby Coll. B61451 British Museum Nat. Hist.) has recently been re-figured (Muir-Wood, 1951, Pl. 4, Figs. 3a–c). It is larger than any of the 829 measured specimens from Cave Dale, which suggests that the latter are unlikely to be topotypes as had been thought possible.

GROWTH CONSIDERATIONS

A plot (not figured) of length against width on arithmetical co-ordinates of the Cave Dale specimens shows an almost rectilinear relation, i.e. growth is nearly isometric. A better fit is obtained by plotting

TABLE 5.—SIGNIFICANCE OF DIFFERENCES BETWEEN KERMACK AND HALDANE LINES

The questions of Table 4 are of the form
$y = \beta x^{\alpha}$ or $\log y = \alpha \log x + \log \beta$
where α = slope and β = intercept of line.

Cave Dale and Treak Cliff

L and W	t (α)	= 0.71	Not significant
	t (log β)	= 1.46	Not significant
T and W	t (α)	= 0.087	Not significant
	t (log β)	= 0	Not significant

Cave Dale and Craven Reef

L and W	t (α)	= 1.74	Not significant
	t (log β)	= 1.28	Not significant
T and W	t (α)	= 5.76	Significant at the 0.1% level of probability

Treak Cliff and Craven Reef

L and W	t (α)	= 0.22	Not significant
	t (log β)	= 0.62	Not significant
T and W	t (α)	= 2.58	Significant at the 2% level of probability

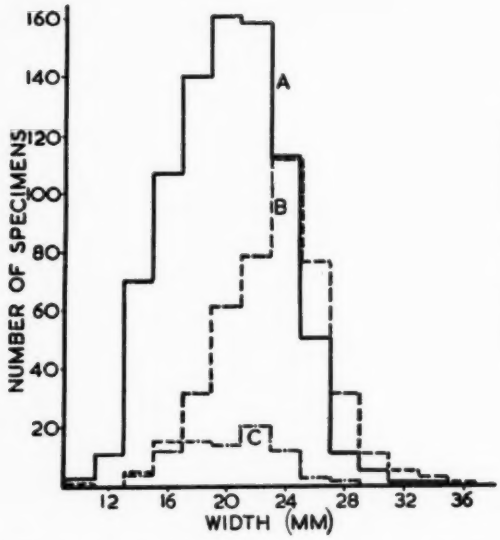

FIG. 2—Width histograms of *Pugnax pugnus* (A) Cave Dale, (B) Craven Reef Belt, (C) Treak Cliff.

on logarithmic coordinates (Fig. 5), indicating allometric growth (Zuckerman and others, 1951, and Parkinson, 1952). Similar linear relations hold for Craven Reef (Fig. 6) and Treak Cliff (not figured).

The T-W relationships (Figs. 7 and 8) also suggest growth allometry, but the

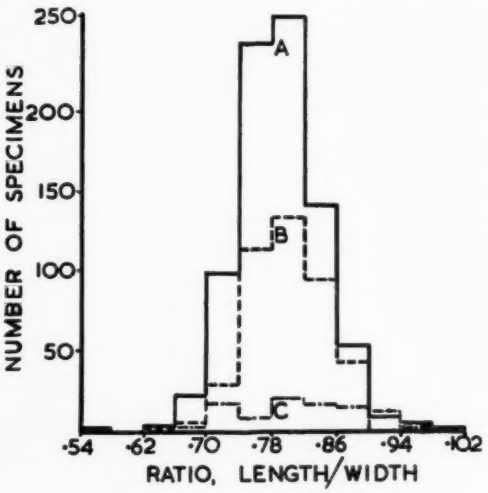

FIG. 3—Histograms of ratio L/W in *P. pugnus* (A) Cave Dale, (B) Craven Reef, (C) Treak Cliff.

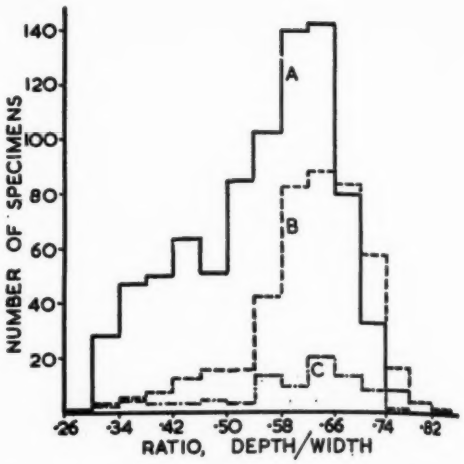

FIG. 4—Histograms of ratio D/W in *P. pugnus*. (A) Cave Dale, (B) Craven Reef, (C) Treak Cliff.

scatter of the points is much greater than in the L-W plot. Growth ratio changes are more pronounced in the D-W plot (Fig. 9), and it is evident that a straight line cannot be drawn centrally through all the points. The scatter in this case tends to be S-shaped with a suggestion possibly of two changes in

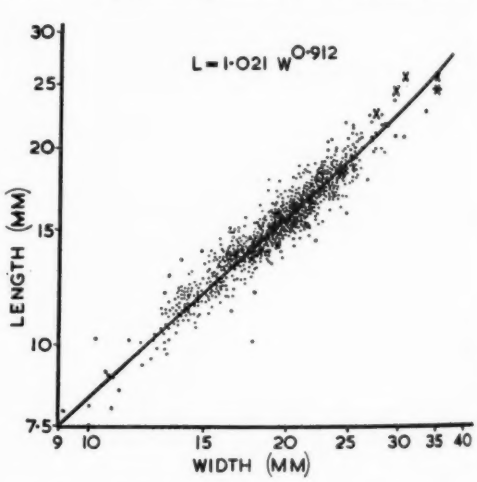

FIG. 5—Relationship between L and W in the Cave Dale collection of *P. pugnus*. In this diagram and in Figs. 6, 7 and 8 the crosses represent specimens from Mich Low and the holotype is denoted by an asterisk. In all graphs the Kermack and Haldane line and the equation to it take no account of the holotype or the specimens from Mich Low.

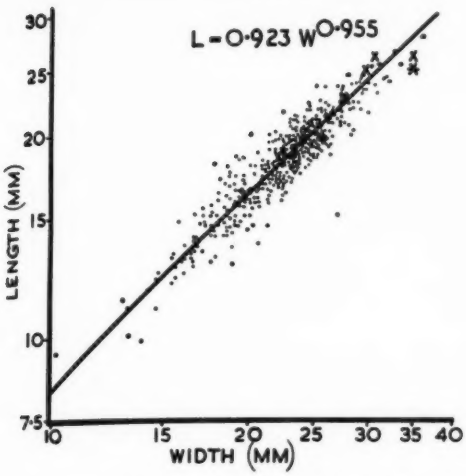

FIG. 6—Relation between L and W of *P. pugnus*. Craven Reef Belt.

growth ratio, one early in life and the other later (at a width between 20 and 25 mm.). Changes in growth ratio have been noted for both *Dielasma hastata* (Parkinson, 1952) and *Schizophoria resupinata* (Parkinson, 1954) at a width of about 20 mm. In the case of *P. pugnus* the scatter of the D-W points is so wide even on logarithmic co-ordinates as to obscure the growth relationship. It might be allometric in three stages, or it could be still more complex.

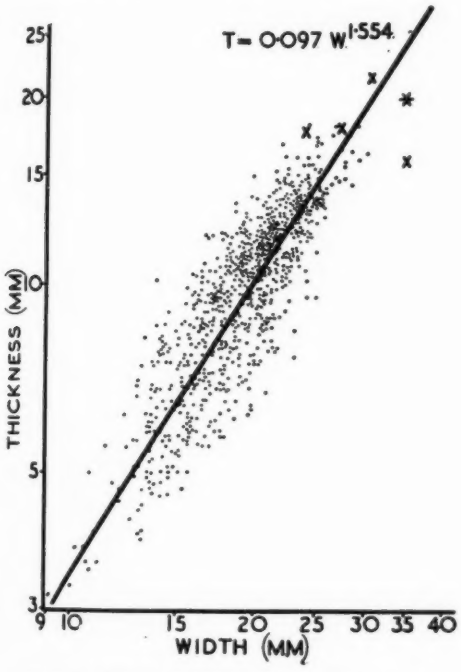

FIG. 7—Relation between T and W of *P. pugnus* Cave Dale.

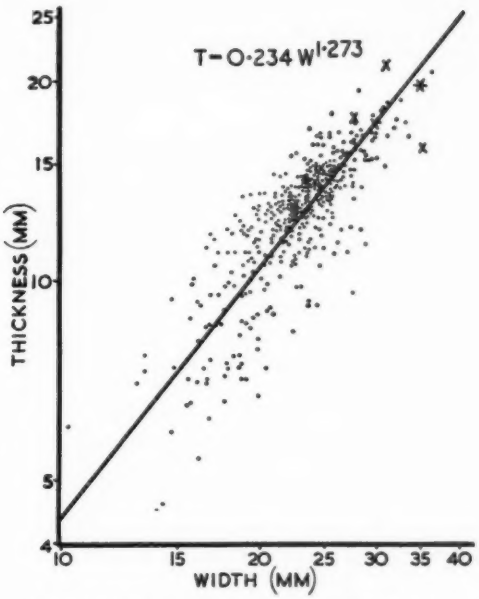

FIG. 8—Relation between T and W of *P. pugnus*, Craven Reef Belt.

NATURE OF THE FREQUENCY DISTRIBUTIONS

The distributions of the length, width and thickness in all cases seem normal. The width histograms (Fig. 2) suggest normal distributions, confirmation being found by the substantially linear plots on arithmetical probability paper. Except for Treak Cliff these are reporduced in Figure 10, together with plots derived from the length and thickness data. The depth distribution is not normal; neither is it lognormal.

Distributions of the L/W ratios are all lognormal as indicated by linear plots on logarithmic probability paper, the one for Cave Dale being reproduced in Figure 11. A substantially lognormal distribution is also shown for the ratio C_M/W (Fig. 11). The D/W and T/W ratio distributions show a strong negative skewness (Fig. 3) and non-linear plots on logarithmic probability paper (Fig. 11).

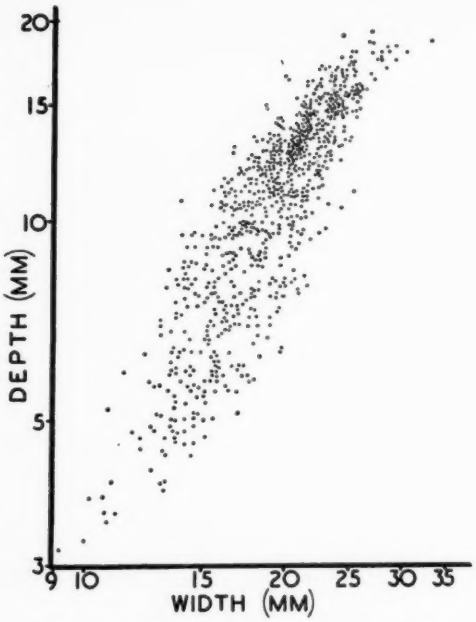

FIG. 9—Relation between D and W of *P. pugnus*, Cave Dale.

SYSTEMATIC DESCRIPTION

Pugnax pseudopugnus, Parkinson, n. sp.
Plate 58, figures 16–20; text-fig. 12

The shell is similar in shape to *P. pugnus*, but is more sharply plicated. The costae are acute and angular, becoming obsolete in the posterior part of the shell. There are usually three, but sometimes two and occasionally four centre plications and costae on the brachial valve and from one to four on each flank. The anterior margin is nearly always simple, layering having been observed in no more than 1% of the specimens examined.

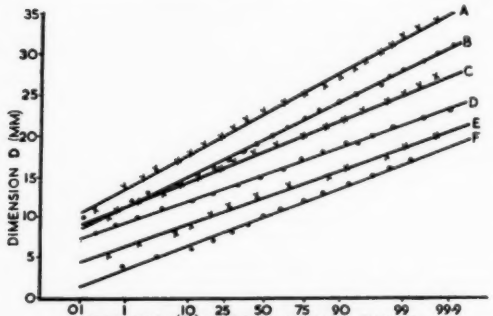

FIG. 10—Distribution of dimensions of *P. pugnus* on arithmetical probability paper. Width is represented by curves A (Craven Reef) and B (Cave Dale), length by C (Craven Reef) and D (Cave Dale), thickness by E (Craven Reef) and F (Cave Dale).

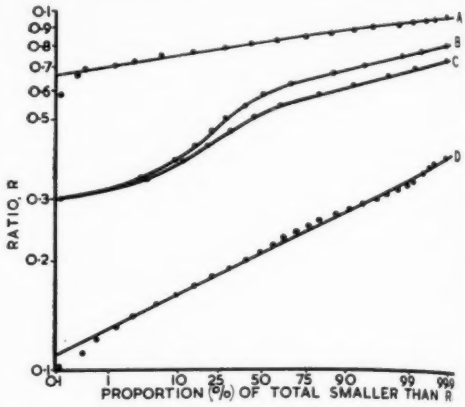

FIG. 11—Distribution of ratios of *P. pugnus* (Cave Dale) on logarithmic probability paper. L/W is represented by curve A, D/W by B, T/W by C and C_M/W by D.

The interior characters (Fig. 12) are similar to those of *P. pugnus*. Dental lamellae are well developed in the pedicle valve. In the brachial valve the hinge plate is divided, the two portions (differing somewhat in shape from those of *P. pugnus*) not being supported by any lamellae. There is no trace of a median septum.

This species is distinguished from *P. pugnus* by its sharper plications and costae, the smaller average number of centre plications, the substantially unlayered nature of the anterior margin, the absence of an incipient median septum and a smaller mean size of shell.

Small specimens of *P. psuedopugnus* resemble *Pugnoides ? triplex* (M'Coy) in having three centre plications in the brachial valve and in the obsolescence of the costae in the posterior part of the shell. They differ from M'Coy's species in the absence of a median septum in the brachial valve.

Holotype.—In the author's collection, from *Dielasma* bed, Treak Cliff, Derbyshire.

VARIATION AND RELATIVE GROWTH IN *Pugnax pseudopugnus*

This species is found in the *Dibunophyllum* zone of England. The writer has collected it from the *Dielasma* bed (Parkin-

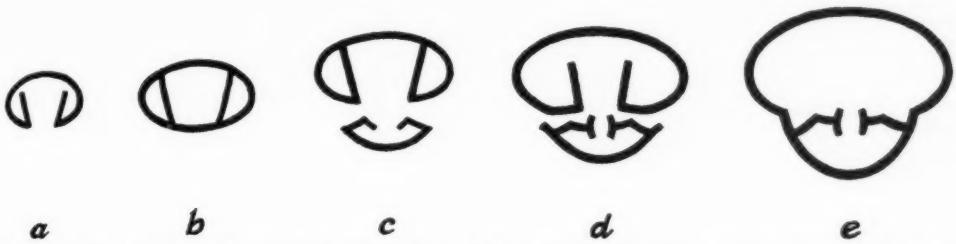

FIG. *12*—Sections through the umbonal region of *Pugnax pseudopugnus*, Treak Cliff, Derbyshire. Total length of specimen 15.6 mm.; width 19.0; thickness 9.5 mm. a, at 0.4 mm. from apex of ventral umbo; b, at 1.1 mm.; c, at 1.6 m.; d, at 2.1 mm.; e, at 2.6 mm.

son 1952, 1954) and other exposures on Treak Cliff, Derbyshire, and he has recognised it in the Geological Survey Collection from Parkhouse Hill, Derbyshire.

Two collections are compared here, one community of 39 specimens from the *Dielasma* bed and the other a composite sample from the Craven Reef Belt, Yorkshire in the Tiddeman collection of Skipton Museum. The statistics of these assemblages are given in Table 6. Tests of significance show no difference between the L/W, T/W and D/W ratios from the two areas.

Scatter diagrams (Figs. 13–17) show that the *Dielasma* bed specimens are all within the range of variation of the Craven Reef assemblage. Growth allometry is clearly shown in the L–W plots (Figs. 13, 14) and the equations of the Kermack and Haldane lines of the two samples do not differ significantly. There is a suggestion of curvature in the scatter of the T-W, T-L and D-W plots resulting possibly from a change in growth ratio at a width of about 10 mm. In Figure 15 the K and H line from the Craven Reef collection does not pass centrally through the points at the lower end of the scale in keeping with this interpretation. The slope of this line differs significantly at the 1% level of probability from that representing the *Dielasma* bed community.

The spread of the points in these diagrams is least in the L-W plot, greater in the T-L plot and still greater in the T-W plot. There is thus a closer correlation between L and W than between the other metrical characters, a fact which could have been brought out still more clearly by plotting the ratios as was done for *P. pugnus* by B. Simpson (1933) and for other brachiopods (Parkinson, 1952 and 1954). It may be a general principle that throughout the life of a brachiopod length and width do not vary independently of each other.

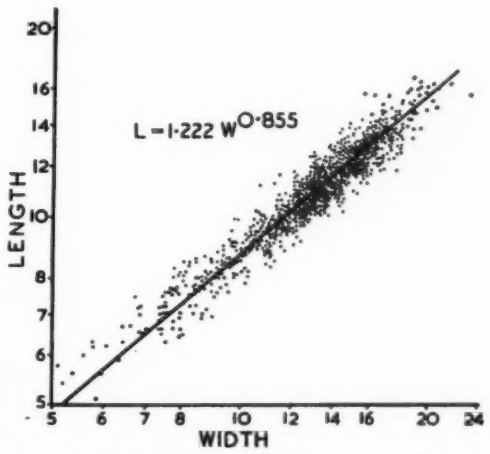

FIG. *13*—Relationship between L and W of *P. pseudopugnus*, *Dielasma* bed, Treak Cliff.

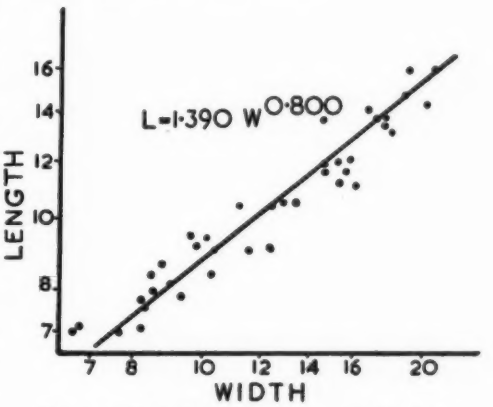

FIG. *14*—Relation between L and W of *P. pseudopugnus* Craven Reef Belt.

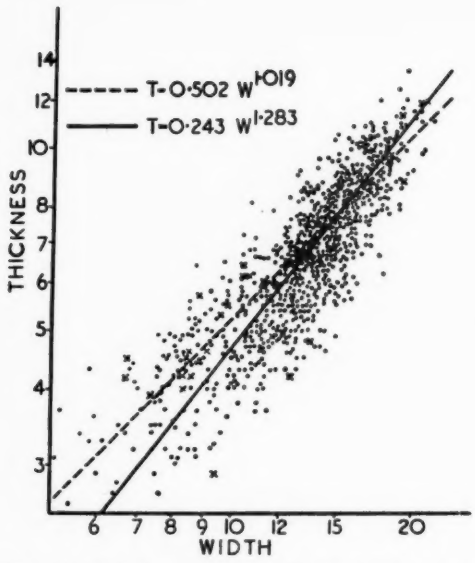

FIG. *15*—Relation between T and W of *P. pseudopugnus*. The dots and continuous line represent the Craven Reef specimens and the crosses and dotted line the *Dielasma* bed specimens.

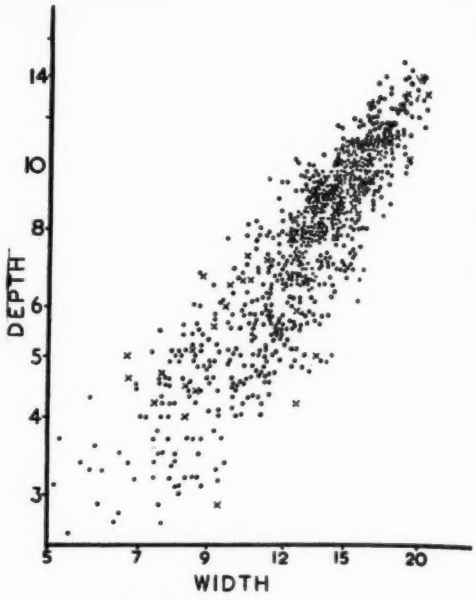

FIG. *16*—Relation between D and W of *P. pseudopugnus*. The dots represent Craven Reef and the crosses the *Dielasma* bed.

Like those of *P. pugnus* the dimensions are distributed normally. Histograms of the width distribution of the two species are drawn in Figure 18 with the normal curves superimposed. If these two curves are combined there is a considerable positive skewness and a suggestion of bimodality. These facts lend objective support for the separation into two species which was made subjectively. The L/W ratio as with *P. pugnus* is distributed lognormally. The T/W distribution, curiously enough, is almost normal, but the D/W and D/L distributions show negative skewness. (These graphs are not reproduced in the paper.)

CONCLUSIONS

The preliminary examinations of a large number of specimens of *Pugnax* cf. *P. pugnus* pointed to the probability that two species only were represented. Subsequent statistical analysis has not raised any doubts on the validity of the initial separation into *P. pugnus* (Martin) and *P. pseudopugnus* n. sp., but it has shown that in the case of *P. pugnus* significant differences exist between assemblages from different areas. These different populations can be regarded as approximating to topodemes since their geological levels are not far apart in time. Insufficient material is available to indicate

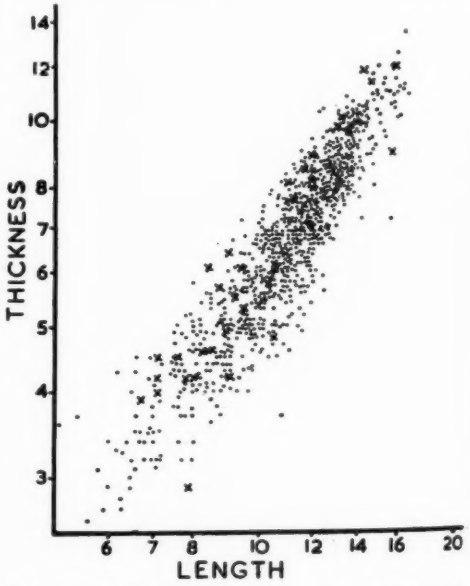

FIG. *17*—Relation between T and L of *P. pseudopugnus*. The dots represent Craven Reef and the crosses the *Dielasma* bed.

TABLE 6.—STATISTICS OF *Pugnax pseudopugnus*

Locality	Character	N	Range mm.	Mean mm.	Standard Deviation
Dielasma bed, Treak Cliff	W	39	6.7 –20.8	13.00	4.130
	L	39	6.7 –15.9	10.64	2.680
	T	39	2.9 –11.9	6.83	2.223
	L/W	39	0.70– 1.06	0.8422	0.0998
	T/W	39	0.31– 0.67	0.5291	0.0799
	D/W	39	0.31– 0.76	0.5938	0.1036
Craven Reef Belt	W	855	5.1 –23.3	13.34	3.003
	L	855	5.4 –16.7	11.15	2.135
	T	855	2.6 –13.5	6.76	1.965
	L/W	855	0.67– 1.14	0.8442	0.0701
	T/W	855	0.31– 7.6	0.5075	0.0797
	D/W	855	0.34– 8.3	0.5897	0.0968

Number of costae on median fold of brachial valve	Number of specimens		Mean number of costae
	Dielasma bed	Craven Reef	
1	0	1	Dielasma bed 3.031
2	2	51	
3	33	778	Craven Reef 2.967
4	4	25	
	39	855	

Equations of Kermack and Haldane lines

Dielasma bed

$L = 1.390\ W^{0.800}$ Log L = 0.800 log W + 0.143
$T = 0.502\ W^{1.019}$ Log T = 1.019 log W − 0.299

Craven Reef Belt

$L = 1.222\ W^{0.855}$ Log L = 0.855 log W + 0.087
$T = 0.243\ W^{1.283}$ Log T = 1.283 log W − 0.615

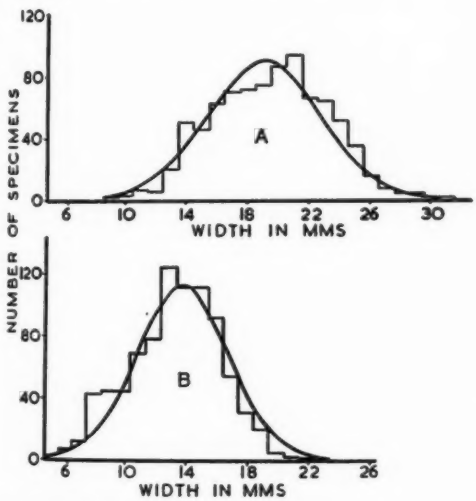

FIG. *18*—Width histograms of (A) *P. pugnus*, Cave Dale and (B) *P. pseudopugnus*, Craven Reef, with the normal curves superimposed.

the extent of difference between different communities in the case of *P. pseudopugnus*, but the available evidence suggests that it is a more uniform species than *P. pugnus* in regard to size and in the number of centre plications. The two species exhibit a similar wide range of variation in shape.

Both species display allometric growth of length in relation to width ($L = \beta W^{\alpha}$), the L/W ratio decreasing with growth ($\alpha < 1$) in each case. This decrease is small for *P. pugnus*, growth being almost isometric. Relative growth of thickness and width is approximately allometric, the T/W ratio increasing with growth at a greater rate in *P. pugnus* than in *P. pseudopugnus*.

This investigation supports G. G. Simpson's plea (1940, and Newell, 1949) for the introduction of the hypodigm into paleontology. The hypodigm of *P. pugnus* would be a sample comprising the specimens em-

ployed in the biometrical study reported here, 1,351 in all, including the holotype. Similarly the hypodigm of *P. pseudopugnus* would encompass the 894 specimens dealt with in the present study.

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MANUSCRIPT RECEIVED JUNE 4, 1953

EXPLANATION OF PLATE 58

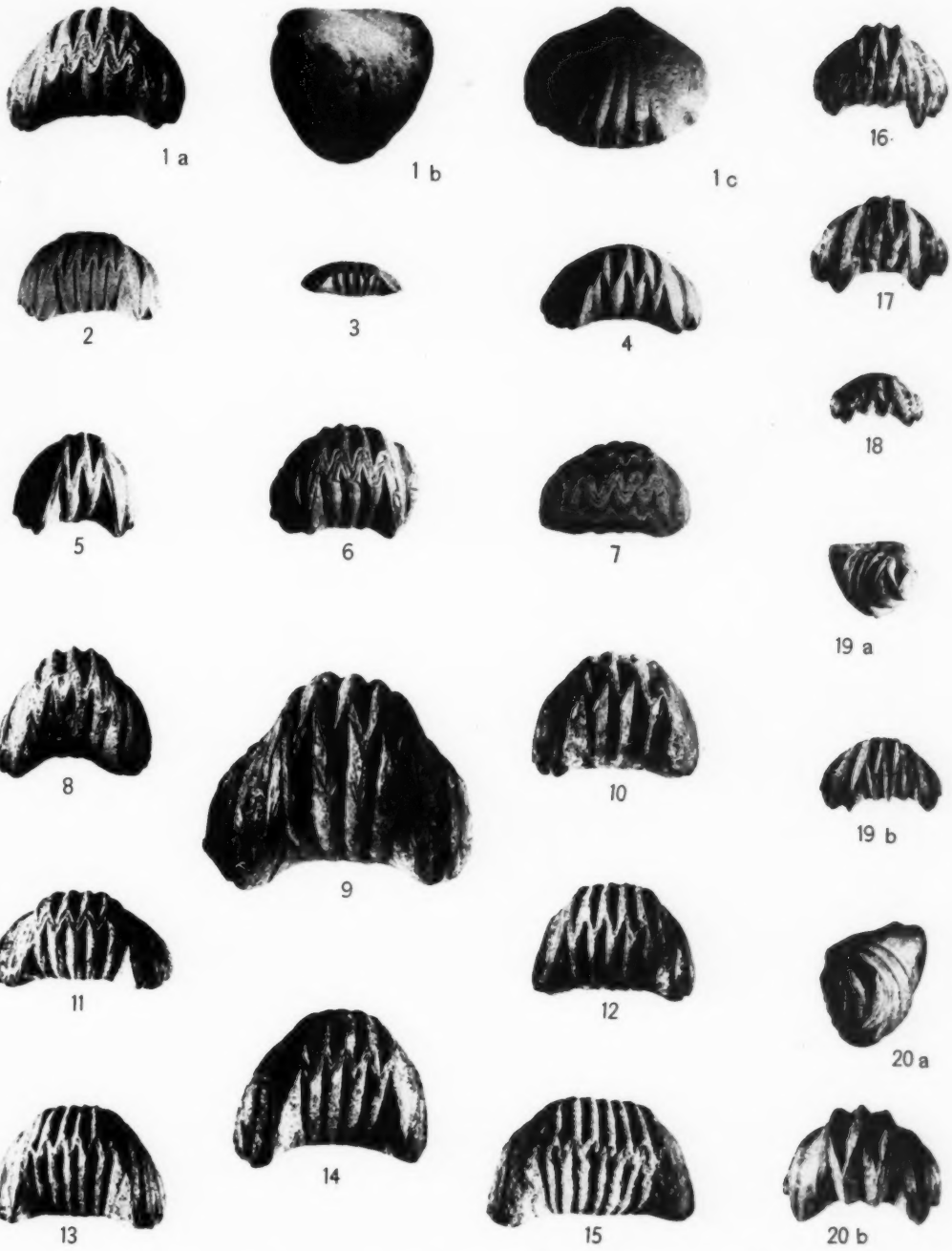
All figures approximately natural size.

FIGS. *1a–c*—*Pugnax pugnus* (Martin) from the Carboniferous limestone of Cave Dale, Castleton, Derbyshire. Anterior, oblique and dorsal views of same specimen. D.P. coll. (p. 564)

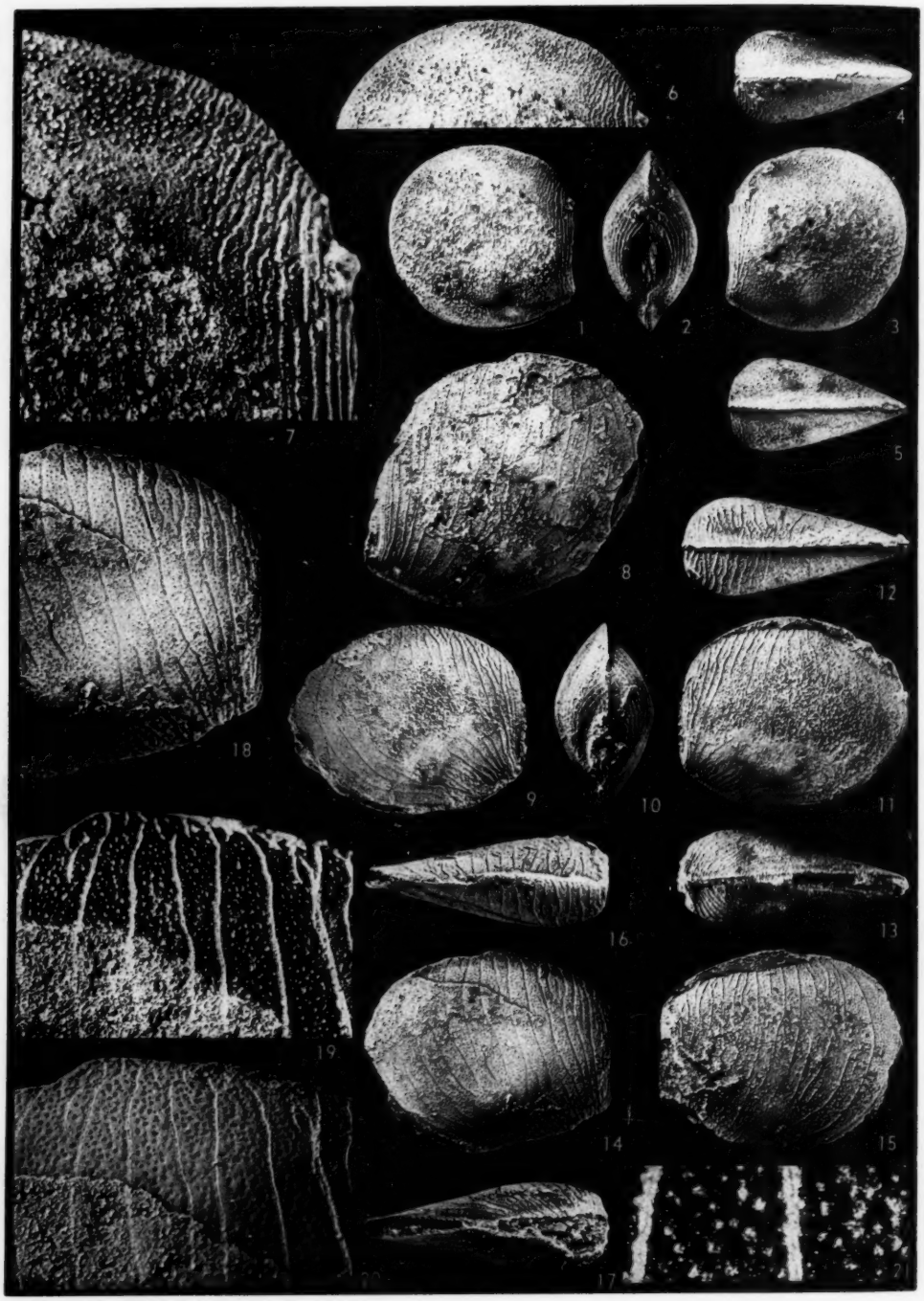
2–15—*P. pugnus*. Anterior views; *2–7* from Cave Dale, Swansea Univ. College coll. *8* from Treak Cliff, D.P. coll. *9–15* from Craven Reef, Yorkshire, Tiddeman coll. Skipton Museum. (p. 564)

16—*Pugnax pseudopugnus* Parkinson, n. sp. Anterior view of holotype from *Dielasma* bed, Treak Cliff, Derbyshire. D.P. coll. (p. 570)

17–20—Paratypes of *P. pseudopugnus* from *Dielasma* bed, *17–18*, anterior views of two specimens; *19a, b*, oblique and anterior views of specimen with four centre plications on brachial valve; *20a, b*, oblique and anterior views of another specimen. D.P. coll. (p. 570)



Parkinson, *Pugnax* from Lower Carboniferous, England



Kesling, new Devonian ostracod

JOURNAL OF PALEONTOLOGY, VOL. 28, NO. 5, PP. 575–580, PL. 59, 1 TEXT FIG., SEPTEMBER 1954

ONCOTECHMONINAE, A NEW SUBFAMILY OF ENTOMOCONCHID OSTRACODS FROM THE MIDDLE DEVONIAN OF NEW YORK

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University of Michigan, Ann Arbor, Michigan

ABSTRACT—Macroscopic ostracods from the Wanakah shale member of the Middle Devonian Ludlowville formation in western New York are assigned to two new genera, *Oncotechmonus* and *Checontonomus*. The first is the type genus of the Oncotechmoninae, a new subfamily of the Entomoconchidae. The two new genera exhibit unusual patterns of ridges which are new to ostracods. The type species of the new genera described are *Oncotechmonus chemotus*, n. sp., and *Checontonomus cophus*, n. sp.

INTRODUCTION

FOUR large ostracods from the Wanakah shale member of the Middle Devonian Ludlowville formation are classified as a new subfamily of the Entomoconchidae, two new genera, and two new species. They belong to the superfamily Entomoconchacea of the suborder Myodocopa.

Although ostracods of the Entomoconchacea are rare, they deserve detailed study because they comprise an extinct superfamily developed early in the history of the Myodocopa. The entomoconchaceans have no rostral incisure; except for this, they have features of the carapace like those of other ostracods of the Myodocopa. There can be little doubt that their assignment to the suborder is correct. The Entomoconchacea has two families, the Entomoconchidae limited to Devonian and Carboniferous and the Cyprosinidae limited to Devonian. Very few specimens of either family have been found. The inadequacy of the fossil record may be related to the ecology of the entomoconchaceans: if they, like the living myodocopans, were free-swimming, their carapaces would have been distributed over a broad area and not concentrated into a small thanatocoenose like that of benthonic ostracods.

The specimens described in this paper were collected in 1942 by Mr. Irving G. Reimann and Mr. Fred W. Wattles, Jr. from Wanakah shale exposures in Erie County, New York, and were deposited in the Buffalo Museum of Science.

The author is very grateful to Dr. P. C. Sylvester-Bradley, who offered helpful suggestions on the classification of these unusual fossils. Photographs on the plate were made with equipment provided by the Horace H. Rackham School of Graduate Studies, University of Michigan.

SYSTEMATIC DESCRIPTIONS

Order OSTRACODA
Suborder MYODOCOPA Sars, 1866

Remarks.—Ostracods of the Myodocopa can be readily distinguished from those of other suborders by their soft parts: they are the only ones with a heart. With one exception, living ostracods of the Myodocopa can be distinguished also by their carapace: when the valves are closed, they have an anterior opening of the carapace variously called rostral incisure, rostral sinus, or gape. The antennules and antennae can protrude through this rostral incisure at all times.

EXPLANATION OF PLATE 59

FIGS. *1–7*—*Checontonomus cophus* Kesling, n. sp. *1–5*, right lateral, anterior, left lateral, dorsal, and ventral views of carapace, holotype, No. E15871, ×4.5. *6*, dorsal part of same viewed from the right, ×7.7. *7*, anterodorsal part of same viewed from the right, ×18. (p. 578)

8–21—*Oncotechmonus chemotus* Kesling, n. sp. *8*, left lateral view of incomplete carapace, paratype, No. E14292*c*, ×4.5. *9–13*, right lateral, anterior, left lateral, dorsal, and ventral views of carapace, holotype, No. E14292*a*, ×4.5. *14–17*, right lateral, left lateral, dorsal, and ventral views of carapace, paratype, No. E14292*b*, ×4.5. *18*, anterior part of same from the right, ×7.6. *19–20*, dorsal part of same from the right; *19* without coating of ammonium chloride, ×14. *21*, dorsal part of same without coating, ×42. (p. 577)

The one living myodocopan genus which lacks a rostral incisure should be mentioned here, inasmuch as it proves that the incisure is not an essential subordinal character. It is *Thaumatocypris*, described from the Recent (G. W. Müller, 1906, p. 41) and known also from Jurassic (Triebel, 1941, pp. 376–77). *Thaumatocypris* is the only genus of the subfamily Thaumatocyprinae G. W. Müller, 1906, of the family Halocypridae Dana, 1853. It agrees with other halocyprids in many details, such as the number of podomeres in the antennule and in the endopodite of the antenna. It has a short straight anterior border between two protuberances which, by their positions, suggest the slightly protuberant anterodorsal and anteroventral angles of *Entomoconchus*.

Superfamily ENTOMOCONCHACEA
Sylvester-Bradley, 1953

Remarks.—Sylvester-Bradley (1953, p. 132) characterized the superfamily simply as: "Macroscopic Myodocopa without rostrum or rostral sinus, usually with a posterior sinus. An oval muscle-scar pattern consists of radiate linear scars."

All entomoconchaceans have a curved hinge line and lack large protuberances or lobes.

Family ENTOMOCHONCHIDAE
Brady, 1868

Remarks.—This family includes *Elpezoe* Přibyl, 1950 (Devonian), *Entomoconchus* McCoy, 1839 (Carboniferous), and the two new genera described below. The inclusion of the new genera apparently requires an emendation of the diagnosis of the family offered by Sylvester-Bradley, who wrote (1953, p. 132): "Entomoconchacea with a straight, vertical anterior margin; left valve larger than the right, overlapping it particularly at the antero-dorsal and anteroventral angles." Although some specimens of the new genera are slightly crushed, the dorsal overlap seems to be right/left. If the reference to overlap is deleted, Sylvester-Bradley's diagnosis will apply to all known genera.

ONCOTECHMONINAE Kesling, n. subfam.

Type genus.—*Oncotechmonus*, n. gen.

Description.—Entomoconchidae with flat or depressed anterior region of the carapace. Posteroventral gape, if present, elongate between the valves, not subcircular, not with protuberant edges. Valves coarsely punctate, ornamented with small ridges more or less concentric around the anterior region.

Remarks.—The two genera assigned to this subfamily have a subcentral projection of low relief, the greatest width distinctly anterior, and, as seen in dorsal view, sides tapering sharply to the posterior end. These characteristics are not regarded at this time, however, as critically important in the subfamily description.

Entomoconchus and *Elpezoe* are excluded from this subfamily by their smooth valves. Both lack a depressed anterior region and a long posteroventral gape, although some specimens of *Entomoconchus* have a posteroventral or posterior siphon.

ONCOTECHMONUS Kesling, n. gen.

Types species.—*Oncotechmonus chemotus*, n. sp.

Description. — Oncotechmoninae with prominent posteroventral and posterior gape between the valves. Greatest width anterior. As seen in dorsal view, lateral surfaces taper sharply from the region of greatest width to the posterior end. Little ridges ornamenting nearly all of lateral surface in each valve.

Remarks.—The ornamentation is very much like that of *Estherites*, a genus of another order of crustaceans, the Conchostraca. This is the first occurrence of this kind of ornamentation known in ostracods. The shape of the carapaces excludes the specimens from the estherians and places them in the entomoconchid ostracods; this association of ornamentation and shape of carapace is not present in either estherians or other ostracods, so the classification depends upon importance of characters. Shape is here regarded as the more important of the two.

Other ostracods with ridges have them arranged in a pattern different from that of *Oncotechmonus*. Some families are characterized by ridges more or less parallel to the length: thus, in most genera and species, the Glyptopleuridae and Barychilinidae have a few distal ridges concentric to the dorsal and free borders and all the others sloping posterodorsal-anteroventral, and the Entomo-

zoidae has ridges nearly horizontal at mid-height and subparallel to the borders dorsad and ventrad, with all ridges convergent toward the ends.

Cyprella, a Carboniferous genus of the myodocopan family Cypridinidae, has ornamentation resembling that of *Oncotechmonus* in shape and in part of the pattern of distribution. Jones and Kirby (1874, p. 35) wrote of *Cyprella:* "The general form is that of *Cypridinella* and *Cypridellina*, with apiculate and indented end and a truncate front . . . but the chief character is a vertical and necessarily annular striation, furrowing, or step-like marking on the carapace." The anterior ridges of *Oncotechmonus* are annular and have furrows along their rear borders which give them a steplike cross-section; but its posterior ridges are concentric to the free border instead of annular. Furthermore, *Oncotechmonus* has no apiculate end.

The name of this genus, an anagram of *Entomoconchus*, is derived from Greek *ογκωτος* ("heaped up"), *εχμα*, n. ("a hinderance, an obstacle"), and *ονος*, m. ("an ass") and refers to the difficult classification of an ostracod with a blunt front like *Entomoconchus* and ornamentation like *Estherites*.

ONCOTECHMONUS CHEMOTUS
Kesling, n. sp.
Plate 59, figures 8–21; text-figure 1

Description.—Carapace large, subelliptical in lateral view, cuneate in dorsal view, and sublanceolate in end view. Valves nearly equal, overlap apparently right/left in the dorsal part and left/right in the ventral part of the carapace. Anterior part of the carapace flat or slightly concave; concave area incomplete on all specimens, but apparently without rostral incisure. Anterior border vertical, straight; dorsal border curved evenly with radius of curvature equal to the height; posterior border curved with radius about one-third the height; posteroventral border curved evenly with radius about equal to the height; and anteroventral border slightly convex, nearly straight. Juncture of the anterior and anteroventral borders slightly protuberant.

Posteroventral gape (Fig. 1) between the valves, extending from a point immediately behind the anteroventral contact of the valves to the posterodorsal part of the carapace. This gape in the same part of the carapace as the siphon in *Entomoconchus;* the two may be comparable structures.

Subcentral projection on each valve, subelliptical in outline, with low relief, nearly flat-topped, dorsally confluent with the rest of the lateral surface. The significance of this structure is not known; the internal surface of the valves has not been seen, so whether this represents the position of the muscle scar remains in doubt. Valve slightly compressed below the subcentral projection.

Surface punctate with punctae of two distinct sizes (Pl. 59, fig. 21), the larger about 25 microns in diameter and the smaller, more munerous, about 4 microns. Surface also ornamented by a pattern of small (40 microns wide) crestlike ridges. In general, the ridges parallel to the anterior border at the front of the valve, perpendicular to the front two-thirds of the dorsal border, perpendicular to the anteroventral border, and concentric to the posteroventral, posterior, and posterodorsal borders. Ridges become faint in the central part of each valve. No ridges cross the subcentral projection, and two or three ridges from the anteroventral part of the valve are sharply curved backward below the projection (Pl. 59, fig. 11). Some ridges in the anterior part of the valve anastomose, and several short ridges are interspersed with the longer ones in the dorsal part. The ridges, particularly those in the anterior region, have a gentle anterior slope and a steep posterior declivity into a shallow groove, so that the shell has the appearance of overlapping, thin, scalelike layers. The anteroventral border ornamented by about 20 small scallops (Fig. 1e) which seem to bear no relation to the adjacent ridges.

Dimensions of the holotype, a carapace: length, 7.4 mm.; height, 6.0 mm.; and width, 3.2 mm. Greatest dimension of paratype 14292*c*, an incomplete carapace: 9.7 mm.

Remarks.—All specimens are pyritized, and interpretation of shell structure is difficult. The pattern of the ridges can be seen on a thin outer layer (Pl. 59, figs. 19–20) that adheres to small areas of the valves. This outer layer, I believe, is only a thin extraneous coating of pyrite and not a replacement of shell material. Parts of the lateral surfaces of all specimens are rough

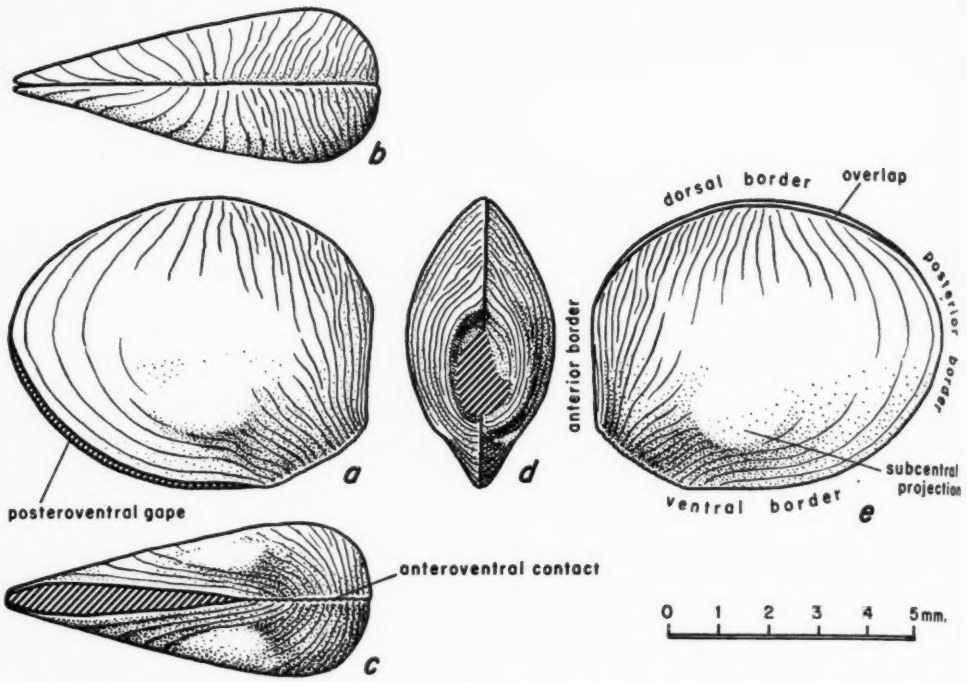

FIG. 1—Reconstruction of *Oncotechmonus chemotus* Kesling, n. sp. *a–e*. Right lateral, dorsal, ventral, anterior, and left lateral views. The cross-hatched area in the anterior view represents imperfect preservation.

where replacement is imperfect.

Unfortunately, nothing is known of the muscle scar or the hingement. In all specimens the dorsal part of the left valve has been thrust under that of the right; the assumed right/left overlap in that part of the carapace may be questioned.

The trivial name of this species is derived from Greek χημη, f. ("a yawning, a gaping") and refers to the posteroventral gape.

Occurrence.—Middle Devonian, Hamilton group, Ludlowville formation, Wanakah member, *Pleurodictyum* bed. Exposure on Bay View Creek between Athol Springs and Bay View, about ¼ mile south of Big Tree Road and ¾ mile east of the shore of Lake Erie, Hamburg Twp., Erie Co., New York. Collected by Mr. Irving G. Reimann.

Types.—Holotype, Buffalo Museum of Science No. 14292*a*. Paratypes, Nos, 14292*b* and 14292*c*.

CHECONTONOMUS Kesling, n. gen.

Type species.—*Checontonomus cophus*, n. sp.

Description.—Oncotechmoninae with narrow posteroventral gape or none. Greatest width anterior. As seen in dorsal view, lateral surfaces taper sharply from the region of greatest width to the posterior end. Little ridges ornamenting the anterior part of each valve, parallel to the straight anterior border.

Remarks.—This genus differs from *Oncotechmonus* in having the posteroventral gape very narrow or absent and in having ornamental ridges only in the anterior part of each valve.

The name of this genus is derived from Greek χεω ("to pour"), κοντος ("short"), and ονομα, n. ("a name") and refers to its composition as an anagram of *Entomoconchus*, to which it is related.

CHECONTONOMUS COPHUS
Kesling, n. sp.
Plate 59, figures 1–7

Description.—Carapace large, subcircular in lateral view, cuneate in dorsal view, and sublanceolate in end view. Valves nearly

equal, overlap right/left in the dorsal part and left/right in the ventral part of the carapace. Anterior part of a carapace deeply depressed as a sublanceolate indentation. Surface of the valves not well preserved within this indentation, but apparently with a low, vertical, irregular ridge along the free edge of each valve (Pl. 59, fig. 2). Anterior border nearly straight, slightly concave in its lower part; dorsal, posterior, and ventral borders curved evenly, nearly circular, the anteroventral border more gently curved, nearly straight. Juncture of the anterior and anteroventral borders distinctly protuberant.

Anterodorsal and ventral parts of the lateral surface concave. Two shallow grooves, convex ventrally, in the ventral concave part of each valve: the first from the anteroventral edge of the subcentral projection to the juncture of the anterior and anteroventral borders, and the second from the ventral edge of the subcentral projection to the anteroventral border.

In the posteroventral part of the carapace, where the overlap reverses, the edges of the valves (Pl. 59, fig. 5), unfortunately, are damaged. It seems impossible to determine in the only specimen found whether the valves have a narrow slitlike gape or are simply tangent.

Subcentral projection on each valve, circular, with low relief, dorsally confluent with the rest of the lateral surface. Valves slightly inflated above the anterior one of the two shallow grooves extending forward and down from the subcentral projection, as mentioned above.

Surface distinctly punctate (Pl. 59, fig. 7). Anterior quarter of both valves ornamented by unusual small crestlike ridges and steep-sided narrow grooves, arranged parallel to the anterior border as seen in lateral view and concentric around the sublanceolate indentation as seen in anterior view. Ornamentation near the anterior border consisting of distinct ridges, rather close-set and subparallel, a few anastomosing; each ridge with a gentle slope forward and a sharp declivity into a narrow groove at the rear, causing the shell material to have the appearance of overlapping laminae. Immediately behind this area, the ornamentation consisting of narrow grooves only; these grooves subparallel to the anterior border, some anastomosing, particularly in the anterodorsal area, and converging toward the anterodorsal border. Grooves extending to the anterodorsal border, there with narrow, short, notchlike grooves interspersed, causing the anterodorsal border to have numerous small scallops (Pl. 59, fig. 7). The rest of the valve apparently smooth; numerous little papillose projections in the dorsal part of the valves are interpreted as pyrite crystals.

Dimensions of the holotype, the only specimen, a carapace: length, 5.9 mm.; height, 5.8 mm.; and width, 3.0 mm.

Remarks.—The only specimen is replaced with pyrite, like the specimens of *Oncotechmonus chemotus* described above. The replacement and weathering of the specimen combine to efface original structures and make interpretation difficult. The posteroventral edges of the two valves are incomplete; a very narrow margin seems to have broken from each valve. It seems impossible to determine whether the narrow slitlike gape present between the damaged edges would persist if the valves were complete.

The trivial name of this species is derived from Greek *κωφος* ("blunt") and refers to the anterior end of the carapace.

Occurrence.—Same age and locality as that given for *Oncotechmonus chemotus*, n. sp. Collected by Mr. Fred W. Wattles, Jr.

Type.—Holotype, the only specimen, Buffalo Museum of Science No. E15871.

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EARLY ORDOVICIAN TRILOBITE FAUNULES FROM QUEBEC AND NEWFOUNDLAND

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ABSTRACT—Two small trilobite faunules, respectively collected in the Gaspé peninsula of Quebec and in Newfoundland, appear essentially equivalent. Although all the species are new, the affinities are with late Cambrian and early Ordovician forms. The latter are given greater weight, hence the faunules are regarded as of Tremadocian age. New genera described are *Borthaspidella*, *Leiobienvillia*, and *Pareuloma;* new species described are *Borthaspidella gaspensis*, *Bienvillia terranovica*, *Lciobienvillia laevigata*, *Pareuloma brachymetopa* (type species), and *P. impunctata*.

INTRODUCTION

THROUGH the courtesy of Dr. Harry B. Whittington, the writer had the opportunity to examine a small collection made in Newfoundland by Dr. Philip Oxley. The fossils were reported to be of Cambrian or Ordovician age. Study of the prepared material revealed several interesting, undescribed trilobites, partly known to the writer from a collection made in eastern Gaspé several years ago. Hence it was deemed opportune to describe the two faunules simultaneously.

The writer is indebted to Dr. Philip Oxley for information concerning the occurrence of the fossils.

Occurrence of the fossils.—The faunule from Gaspé was collected by the writer from dark, granular limestone interstratified with shale at Cap des Rosiers; more precisely, in the sea cliffs 100 yards east of the brook crossing the village. All the fossils came from a single bed, containing fairly common, but highly fragmentary trilobite material. Only a few identifiable specimens could be recovered. The shales in the vicinity have long been known for their graptolite fauna, recently redescribed by Bulman (1950). The graptolites are of Tremadocian age; however, no study of the local structure was made, hence the relative stratigraphic position of the triobite beds and the graptolite-bearing shales was not ascertained.

Dr. Oxley supplied the following information about the faunule collected in Newfoundland. The locality is on the south side of Broom Point at the outlet of Western Brook. The fossils were recovered from one small limestone lens interbedded with dark argillites, bearing dendroid graptolites. Dr. Oxley states that the fossils were definitely collected from regularly bedded strata, not from a boulder. The rock is a rather light gray, crystalline, highly fossiliferous limestone.

Composition of the faunules.—The faunule from Gaspé includes:

Lingulella, sp. undet.
Borthaspidella gaspensis, n. gen., n. sp.
Pareuloma brachymetopa, n. gen., n. sp.
Shumardia, sp. undet.

The faunule from Newfoundland includes:

Lingulella, sp. undet.
Undetermined gastropod, cf. *Semicirculatea*
Agnostid, gen. and sp. undet.
Bienvillia terranovica, n. sp.
Borthaspidella gaspensis, n. gen., n. sp.
Leiobienvillia laevigata, n. gen., n. sp.
Pareuloma brachymetopa, n. gen., n. sp.
P. impunctata, n. sp.

The equivalence of the two faunules seems well established by the presence of two common species, *Borthaspidella gaspensis* and *Pareuloma brachymetopa*.

The brachiopod and the gastropod cannot at present be used for correlation; the *Lingullela* is of the type common in most Upper Cambrian and Lower Ordovician formations, while little is known about the specific characters and stratigraphic distribution of primitive gastropods. Hence the age of the faunules must essentially be established on the basis of the trilobites.

Shumardia is exclusively known from Ordovician rocks. The agnostid is insuffi-

ciently known to supply a basis for correlation. *Pareuloma* and *Borthaspidella* are new genera, but their affinities are with the Ordovician *Euloma* and *Borthaspis*, respectively. *Bienvillia* was so far known only from the late Cambrian, but there is no reason why *Bienvillia* itself, and its close relative *Leiobienvillia*, could not range into the early Ordovician, where trilobites of this type, e.g., *Desmetia* and *Moxomia*, are present. Thus the whole of the evidence favors an early Ordovician (Tremadocian) age of the faunules.

Identical faunules are not known to the writer from other localities. A faunule that bears some resemblance to the present ones was collected by the Sven Hedin expedition to northwest China and described by Troedsson (1937). One of the species from Troedsson's locality 20, *Symphysurus? anderssoni*, is certainly a near relative of *Borthaspidella gaspensis*, and another, *Shumardia longifrons*, closely resembles the species collected in Gaspé. Troedsson regarded the faunule from locality 20 as Ordovician. In conclusion, it may be stated that the faunules here described are of Tremadocian age, and the Cambrian affinities of several forms are rather suggestive of the lower Tremadoc.

Disposition of material.—The fossils from Gaspé were deposited in the U. S. National Museum; those from Newfoundland in the Museum of Comparative Zoology at Harvard University.

SYSTEMATIC DESCRIPTIONS

Family AGNOSTIDAE Jaekel

Agnostid, gen. and sp. undetermined

Plate 61, figures 13, 14

Available material.—Two well-preserved pygidia.

Description.—Pygidium strongly convex, well rounded posteriorly, with deep marginal furrow and wide border. All other furrows almost entirely obsolete on external surface, faintly visible on cast of interior. Axial lobe poorly defined even on the internal cast except at the anterior and posterior ends where a faint dorsal furrow is visible even on the outer surface. Axial lobe pointed at posterior end, terminating at a distance from marginal furrow equal to width of border. Axial lobe divided by two extremely faint transverse furrows into three lobes; lengths of two first lobes about equal. An elongated tubercle occupies the whole length of the second lobe and is visible even on the outer surface.

Surface smooth. Length of pygidium 3.4 mm., width 3.2 mm.

Remarks.—Although the species is represented by excellent pygidia, no reliable generic assignment can be made in the absence of the cephalon. The almost obsolete pygidial furrows indicate a pattern similar to that of the Upper Cambrian genus *Lotagnostus*.

Occurrence.—Broom Point, Newfoundland.

Disposition of material.—MCZ 5124.

Family SHUMARDIIDAE Lake

Genus SHUMARDIA Billings, 1862

SHUMARDIA, sp. undet.

Plate 60, figure 16

Available material.—Two cranidia, one of which is fairly well preserved.

Description.—Cranidium approximately semicircular, almost twice wider than long. Glabella narrow and long, expanded forward, pointed in front; dorsal furrow deep and wide posteriorly, becoming shallower and narrower around frontal portion of glabella; occipital furrow shallow but distinct. Surface smooth. Length of cephalon 1.8 mm., width 3.3 mm.

Remarks.—The species differs considerably from *S. granulosa* Billings and *S. pusilla* (Sars) in the narrowness of the glabella. In this character it resembles *S. longifrons* Troedsson from northwestern China. The present form is not named, as the writer does not believe in the parctice of basing species on one or two individuals, unless perfectly preserved and sharply distinct from known forms.

Occurrence.—Cap des Rosiers, Gaspé peninsula, Quebec.

Disposition of material.—USNM 123460.

Family OLENIDAE Burmeister

Genus BIENVILLIA Clark, 1924

BIENVILLIA TERRANOVICA Rasetti, n. sp.

Plate 61, figures 7–12

Available material.—Numerous cranidia and a few free cheeks well preserved in crystalline limestone.

Description.—Cranidium of low convex-

ity; all furrows shallow. Glabella subquadrate, rounded at anterior angles; dorsal furrow shallow, but uniformly impressed all around glabella. Two pairs of faint glabellar furrows visible, sometimes a trace of a third; furrows impressed only at the sides, oblique, narrow, forming identical pattern as in *Peltura* or *Protopeltura*. Occipital furrow straight, better impressed than glabellar furrows; occipital ring short (sag.), bearing a small node. Fixed cheeks slightly convex, downsloping; frontal area* undifferentiated, convex, downsloping; palpebral lobes small, slightly elevated, distant from glabella about $\frac{1}{4}$ glabellar width, located somewhat back of anterior end of glabella; a bare trace of ocular ridges visible. Anterior facial sutures convergent, forming well-rounded anterior cranidial outline; posterior branch almost straight from eye to margin. Furrow on posterior limbs moderately deep. Surface smooth. Length of larger cranidia 4.4 mm., width between tips of posterior limbs 6.8 mm. Free cheek without distinct border; genal angle probably not produced into spine.

Remarks.—This species presents all the essential characters of the type species, *B. corax* (Billings), differing chiefly in the shallowness of all furrows and the lack of the narrow (sag.) anterior border present in *B. corax*. To facilitate comparison, a topotype specimen of *B. corax* is also figured (Pl. 61, fig. 15). The genus is obviously a close relative of *Peltura*, *Protopeltura*, and similar Olenidae of the Acado-Baltic province.

Occurrence.—Broom Point, Newfoundland.

Types.—Holotype: MCZ 5125. Paratypes: MCZ 5126.

Genus LEIOBIENVILLIA Rasetti, n. gen.

Description.—Known from the cranidium alone. Cranidium similar to *Bienvillia*, characterized by almost complete disappearance of furrows on external surface, entirely convex, subtrapezoidal, rounded in front, about twice wider than long. Palpebral lobes small, anteriorly situated, more distant from the glabella than in *Bienvillia*. Anterior and posterior branches of facial sutures presenting little change in direction. Dorsal and glabellar furrows visible on interior surface, showing identical pattern as in *Bienvillia*.

Type species.—*Leiobienvillia laevigata* Rasetti, n. sp.

Stratigraphic and geographic range.—Known only from the early Ordovician of Newfoundland.

Remarks.—In outer appearance, this trilobite bears a remarkable similarity to *Kingstonia*, *Leiocoryphe* and other smooth Upper Cambrian genera. However, the analogy is purely negative, being based on the lack of furrows. The shape of the glabella and glabellar furrows, visible on the internal surface, unmistakably indicates a member of the Olenidae closely related to *Bienvillia*.

LEIOBIENVILLIA LAEVIGATA Rasetti, n. sp.
Plate 61, figures 3–6; text-figure 3

Available material.—Several cranidia well preserved in crystalline limestone.

Description.—Cranidium of almost uniform convexity. Glabella $\frac{3}{4}$ the cranidial length; glabellar outline and occipital furrow barely visible on outer surface in whitened specimens under proper lighting. Glabellar furrows entirely obsolete on outer surface; three pairs distinctly marked on interior cast, showing same pattern as in *Bienvillia*, *Peltura* and related genera. Palpebral lobes small and but slightly elevated, distant from the glabella almost half glabellar width and situated slightly back of anterior end of glabella. Posterior angles of cranidium sharp; furrow on posterior limbs shallow on interior cast, barely indicated on outer surface. Length of holotype cranidium 3.3 mm., width 5.5 mm. Surface smooth.

Occurrence.—Broom Point, Newfoundland.

Types.—Holotype: MCZ 5127. Paratypes: MCZ 5128.

Family ?PTYCHOPARIIDAE Matthew
Genus PAREULOMA Rasetti, n. gen.

Description.—Glabellar length half the length of cranidium; glabella slightly tapered, truncated in front, defined by a dorsal furrow deep and wide at the sides, narrow and shallow anteriorly; two pairs of glabellar furrows impressed at the sides. Occipital furrow deep, occipital ring simple. Fixed

* The term "frontal area" is used to designate collectively the preglabellar field, marginal furrow, and border.

cheeks as a whole convex; palpebral lobes small, almost at level of anterior end of glabella; distance from glabella about equal to glabellar width; ocular ridges well marked, transverse; preglabellar field convex and downsloping, with a faint median boss; marginal furrow in type species with a series of pits; border distinct. Anterior facial sutures divergent, turning inward after crossing marginal furrow; posterior branch almost straight; posterior limbs deeply furrowed, considerably wider (tr.) than occipital ring.

Pygidium wide and short, of usual ptychopariid type; axis about $\frac{3}{4}$ of pygidial length, furrowed; pleural lobes with furrows and grooves.

Type species.—*Pareuloma brachymetopa* Rasetti, n. sp.

Stratigraphic and geographic range.—Known only from the early Ordovician of Newfoundland.

Remarks.—This trilobite has a decidedly primitive ptychopariid aspect; were its associations not known, it might readily be taken for a Middle Cambrian form, such as *Acrocephalops* or *Bolaspis*. It certainly represents a late ptychopariid, here tentatively placed in the family Ptychopariidae construed in a wide meaning. On the other hand, there are numerous features strongly suggestive of the early Ordovician genus *Euloma*, especially the shape and lobation of the glabella and the series of pits in the anterior marginal furrow. The main differences are the small size of the glabella, corresponding great width of the fixed cheeks, and the small size and anterior position of the palpebral lobes in the new genus as compared with the Scandinavian species *Euloma ornatum* Angelin. An English species, *E. monile* (Salter) (redescribed and figured by Lake, 1940), is intermediate between *Euloma ornatum* and *Pareuloma brachymetopa* in almost all characters; the position and size of the palpebral lobes, however, favor Lake's generic assignment rather than reference to the new genus. There is but little doubt in the writer's mind that *Pareuloma* and *Euloma* are closely related.

PAREULOMA BRACHYMETOPA Rasetti, n. sp.
Plate 60, figures 1–8; text-figure 2

Available material.—Known from a number of cranidia, two hypostomas, and two pygidia.

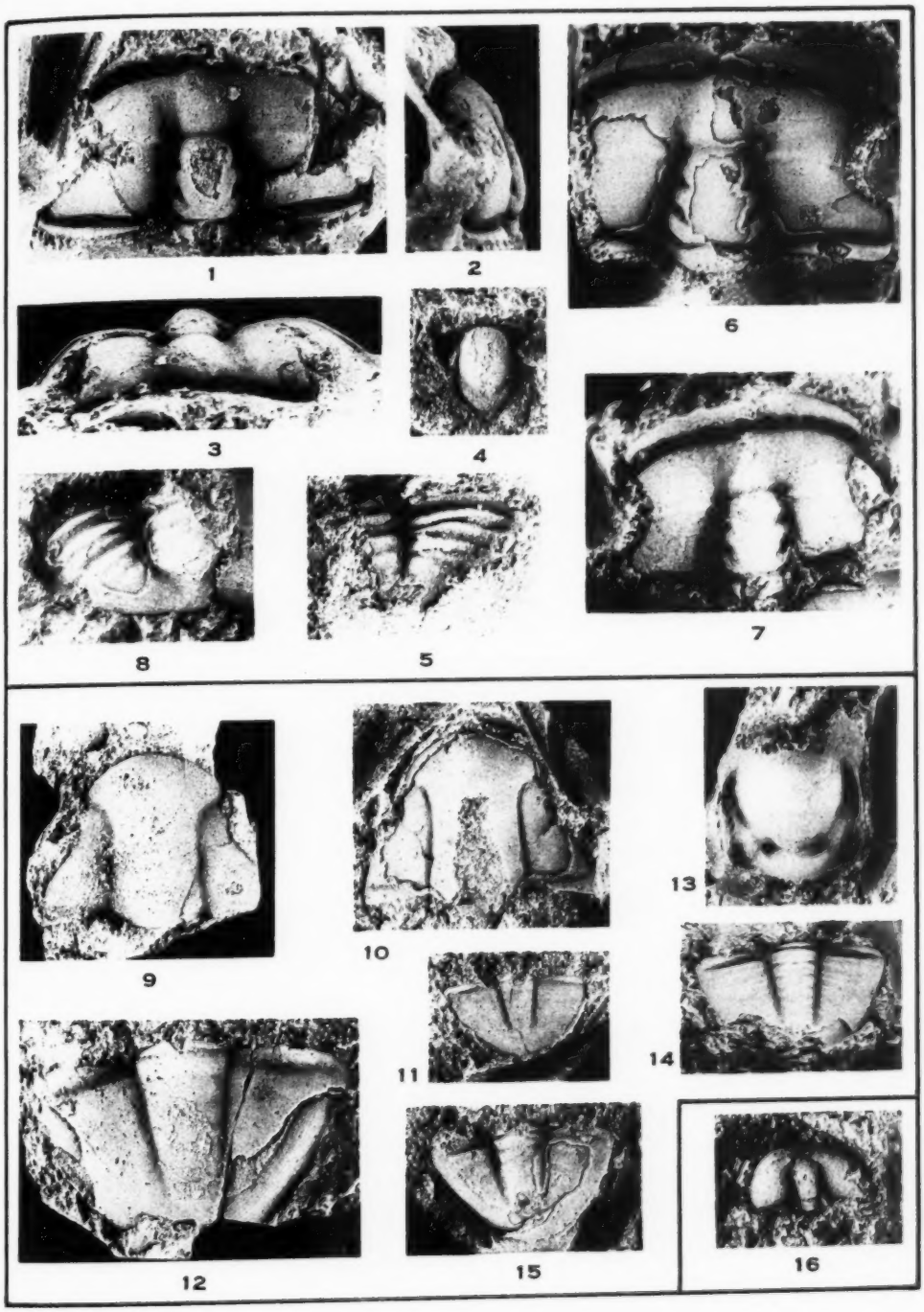
Description.—Features included in the generic diagnosis are not mentioned. Glabella faintly defined anteriorly, with deep glabellar furrows at the sides; dorsal furrows deepened into a pair of pits at the anterior angles of the glabella; occipital ring rather long (sag.), bearing a small node. Preglabellar field of considerable convexity, especially on median line where it forms a boss joining with little change the longitudinal profile of the glabella. Marginal furrows rather deep, marked by a series of pits, about 8 to 10 on each side. Border slightly convex, about $\frac{1}{4}$ as wide (sag.) as the preglabellar field. Fixed cheeks convex, rising above the dorsal furrow but not as high as the glabella, distally downsloping; palpebral lobes very narrow and short, slightly elevated above the surface of the cheeks, set off by faint palpebral furrows. Posterior limbs wide (tr.), with a deep, wide marginal furrow; posterior border showing geniculation about halfway from dorsal furrow; end of posterior limb

EXPLANATION OF PLATE 60

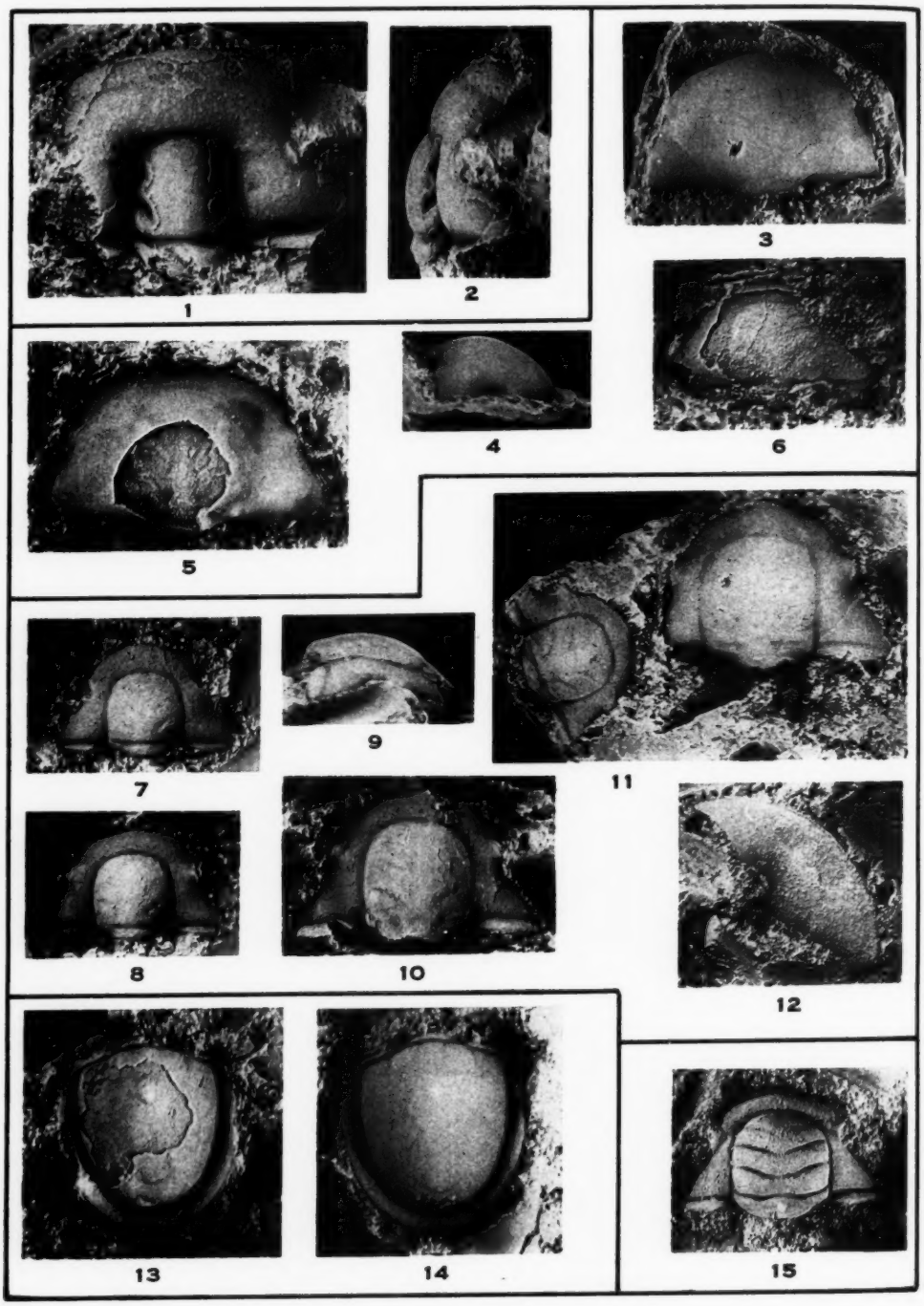
FIGS. *1–8*—*Pareuloma brachymetopa* Rasetti, n. gen., n. sp. *1–3*, Dorsal, lateral and frontal views of cranidium, ×3; USNM 123461, holotype. Cap des Rosiers, Quebec. *4*, Hypostoma, ×3; USNM 123462, paratype. Cap des Rosiers, Quebec. *5*, Fragmentary pygidium, ×5; USNM 123462, paratype. Cap des Rosiers, Quebec. *6*, Partly exfoliated cranidium, ×5; MCZ 5129a, paratype. Broom Point, Newfoundland. *7*, Exfoliated cranidium, ×5; MCZ 5129b, paratype. Broom Point, Newfoundland. *8*, Fragmentary, partly exfoliated pygidium, possibly belonging to *P. impunctata*, ×5; MCZ 5129c. (p. 584)

9–15—*Borthaspidella gaspensis* Rasetti, n. gen., n. sp., ×3. *9*, Cranidium; USNM 123463, holotype. Cap des Rosiers, Quebec. *10*, Exfoliated cranidium; USNM 123464, paratype. Cap des Rosiers, Quebec. *11*, *12*, Pygidia; USNM 123464, paratypes. Cap des Rosiers, Quebec. *13*, Exfoliated hypostoma; MCZ 5132a, paratype. Broom Point, Newfoundland. *14*, *15*, Exfoliated pygidia; MCZ 5132b–c, paratypes. Broom Point, Newfoundland. (p. 587)

16—*Shumardia*, sp. undet. Cranidium, ×5; USNM 123460. Cap des Rosiers, Quebec. (p. 582)



Rasetti, Early Ordovician trilobites



Rasetti, Early Ordovician trilobites

rounded, marginal furrow turning slightly forward.

Hypostoma (assigned to the species on account of association with cranidia at both localities) with main body subovate, with a pair of shallow, oblique furrows almost meeting mesially; anterior wings triangular, connected through narrow (sag.) anterior border; lateral and posterior border fairly wide; posterior end rather sharply pointed.

Pygidium represented by two incomplete specimens. Width somewhat more than twice the length; axis elevated, about $\frac{3}{4}$ length of pygidium, showing three rings plus terminal section; extended into a faint postaxial ridge. Pleural lobes convex; three pairs of furrows and two pairs of grooves well impressed; marginal furrow and border indistinct; posterior outline rounded.

Length of largest cranidium observed 23 mm.; length of pygidium 3.6 mm., width 8.0 mm. Surface of cranidium smooth, of pygidium finely granulated.

Occurrence.—Rather common at Broom Point, Newfoundland; rarer at Cap des Rosiers, Quebec. The latter is the type locality.

Types.—Holotype: USNM 123461. Paratypes (from Newfoundland): MCZ 5129. Paratypes (from Gaspé): USNM 123462.

Pareuloma impunctata Rasetti, n. sp.
Plate 61, figures 1, 2

Available material.—A few fragmentary cranidia lacking the test.

Description.—Glabella as in *P. brachymetopa* but proportionately somewhat larger with respect to other cranidial parts; width of fixed cheeks at palpebral lobes only $\frac{3}{4}$ of glabellar width. Palpebral lobes possibly larger than in *P. brachymetopa;* frontal area convex, downsloping, faintly divided by marginal furrow into preglabellar field and border; width (sag.) of border about half length (sag.) of preglabellar field; no pits in marginal furrow. Anterior facial sutures less divergent than in *P. brachymetopa*, anterior angles of cranidium more widely rounded; posterior branch directed more definitely outward; posterior limbs incompletely preserved. Upper surface not preserved; interior cast showing numerous granules. Length of holotype cranidium 6.2 mm.; fragments indicate individuals twice this size.

Remarks.—Notwithstanding the numerous differences, the species seems closely related to *P. brachymetopa* and can be at least provisionally placed in the same genus, especially as it would not be advisable to erect a new genus on such fragmentary material.

Occurrence.—Rare at the Broom Point locality.

Types.—Holotype: MCZ 5130. Paratypes: MCZ 5131.

Family Asaphidae Burmeister
Genus Borthaspidella Rasetti, n. gen.

Description.—Cranidium and pygidium of low convexity. Glabella parallel-sided in the posterior two-thirds, suddenly expanding forward in the anterior third, reaching the front of the cranidium; occipital and glabellar furrows obsolete. No frontal area; palpebral lobes small, close to dosal furrow at anterior end, on a transverse line through anterior third of glabella. Anterior branch of facial suture following outline of glabella, posterior branch first directed outward and backward, then backward; posterior angles of cranidium fairly sharp; posterior marginal

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Explanation of Plate 61

Figs. *1, 2*—*Pareuloma impunctata* Rasetti, n. gen., n. sp. Dorsal and lateral views of exfoliated cranidium, ×5; MCZ 5130, holotype. Broom Point, Newfoundland. (p. 585)

3–6—*Leiobienvillia laevigata* Rasetti, n. gen., n. sp., ×6. *3, 4*, Dorsal and lateral views of cranidium; MCZ 5127, holotype. Broom Point, Newfoundland. *5*, Cranidium, with glabella partly exfoliated; MCZ 5128a, paratype. Broom Point, Newfoundland. *6*, Exfoliated cranidium; MCZ 5128b, paratype. Broom Point, Newfoundland. (p. 583)

7–12—*Bienvillia terranovica* Rasetti, n. sp., ×5. *7, 8*, Cranidia; MCZ 5126a–b, paratypes. *9, 10*, Lateral and dorsal views of cranidium; MCZ 5126c, paratype. *11*, Two cranidia, the larger being the holotype; MCZ 5125. *12*, Free cheek; MCZ 5126d, paratypes. All specimens from Broom Point, Newfoundland. (p. 582)

13, 14—Agnostid, genus and species undetermined, ×8. *13*, Partly exfoliated pygidium. *14*, Pygidium. MCZ 5124a–b. Broom Point, Newfoundland. (p. 582)

15—*Bienvillia corax* (Billings). Cranidium, ×5; USNM 123465, plesiotype. Upper Cambrian (Trempealeauian) boulder in Levis conglomerate, Levis, Quebec. (p. 583)

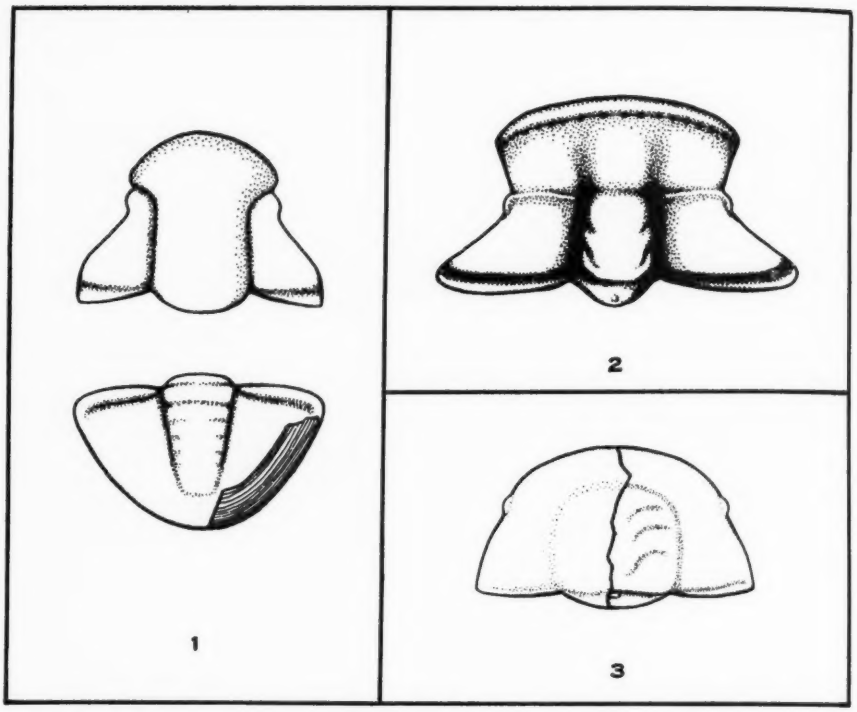

FIG. *1—Borthaspidella gaspensis* Rasetti, n. gen., n. sp. Cranidium and pygidium, ×3. Part of pygidium exfoliated to show extent of doublure. (p. 587)
2—Pareuloma brachymetopa Rasetti, n. gen., n. sp. Cranidium, ×5. (p. 584)
3—Leiobienvillia laevigata Rasetti, n. gen., n. sp. Cranidium, ×6. Right half of cranidium exfoliated to show furrows on internal surface. (p. 583)

furrow faintly impressed.

Pygidium approximately semicircular, slightly convex, without marginal furrow or border. Axis well defined laterally, merging into the general slope posteriorly, faintly annulated; pleural lobes smooth except for the anterior marginal furrow.

Type species.—Borthaspidella gaspensis Rasetti, n. sp.

Stratigraphic and geographic range.—Known from the early Ordovician of Quebec, Newfoundland, and possibly, northwestern China.

Remarks.—The present genus seems most closely related to *Borthaspis* Stubblefield, 1951 (=*Psilocephalus* Salter, 1866; not Swainson, 1839), represented by the type species, *B. innotata* (Salter) redescribed and figured by Lake (1942). The pygidia are substantially identical; the cranidia differ in that the glabella of *Borthaspidella* is better defined by the dorsal furrow, narrower posteriorly, and expands suddenly in the anterior third, while it is poorly defined and essentially parallel-sided in *Borthaspis*. It is also possible that *Borthaspis* still has a residual frontal area, although Lake was not able to establish this point with certainty owing to the almost obsolete condition of the anterior part of the dorsal furrow and the poor preservation of the specimens of *B. innotata*.

Other close relatives are *Platypeltoides* Přibyl (=*Platypeltis* Callaway, 1877; not Fitzinger, 1835) and *Psilocephalina* Hsü, 1948 (not Stubblefield, 1951). Unfortunately, the writer was unable to examine the publication where the type species of *Psilocephalina* is described. *Borthaspidella* is probably also related to *Symphysurus* and similar genera, which share with the new genus the lack of the frontal area; however, in *Symphysurus* the palpebral lobes are much larger and more posterior in position and

the whole cranidium has much greater convexity.

The writer would tentatively assign to *Borthaspidella* a species described by Troedsson (1937) as *Symphysurus? anderssoni*. The cranidia of the two species are remarkably similar; among the pygidia figured by Troedsson, who was unable to assign them with certainty to any one of several similar cranidia, are some which seem hardly distinguishable from the pygidium of *Borthaspidella gaspensis*. All the above-mentioned genera occur in the Tremadocian.

BORTHASPIDELLA GASPENSIS Rasetti, n. sp.
Plate 60, figures 9–15; text-figure 1

Available material.—A few cranidia, several pygidia, and two hypostomas.

Description.—Glabella with undifferentiated occipital ring slightly tapering from posterior margin to midlength, rapidly expanded in anterior third, reaching a maximum width equal to $\frac{2}{3}$ of length. Dorsal furrow shallow but clearly demarcated on outer surface, fairly deep on interior cast. Other characters of cranidium as in generic diagnosis. Hypostoma assigned to the species subrectangular; anterior part not wholly preserved, laterally forming a wide, flat border followed by an indentation of the margin. A similar structure of the hypostomal margin is observed in *Niobe* and related aphid genera (illustrated in Lake, 1942). Opposite the indentation, a pair of furrows curve inward, form a pair of deep pits, and merge mesially into a shallow transverse furrow. There is also a pair of wide, shallow depressions within the posterolateral angles; posterior border broken off in available specimens.

Pygidium 1.7 times wider than long; axis straight-sided, moderately tapered, defined by fairly deep dorsal furrow anteriorly, poorly defined at rear, showing about six progressively shallower furrows on inner surface, only an indication of two or three on outer surface; length of axis about $\frac{2}{3}$ of pygidial length. Pleural lobes slightly convex, lacking marginal furrow and border, showing only anterior furrow on outer surface, traces of several pairs of furrows on interior cast; width of doublure about $\frac{1}{4}$ of pygidial length.

Surface of test smooth. Length of largest cranidium 8 mm., of largest pygidium 10 mm.

Occurrence.—Fairly common at both the Cap des Rosiers and Broom Point localities (former is type locality). Only pygidia and one hypostoma were recovered from the Broom Point locality.

Types.—Holotype: USNM 123463. Paratypes (from Cap des Rosiers): USNM 123464. Paratypes (from Broom Point): MCZ 5132.

MANUSCRIPT RECEIVED JANUARY 25, 1954

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KINGDOM OF ORGANISMS NAMED PROTISTA

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ABSTRACT—Advancement in knowledge, especially during recent decades, has served so effectually to obliterate the boundary between lower types of supposed plants and animals that classification of these organisms given in most botanical and zoological textbooks is outmoded. Since many fossils represent the "no man's land" that strides or lies closely adjacent to the broken down fence, the problem of revised classification is of interest to paleontologists. The term Protista (Haeckel, 1866) is available for designation of a separate kingdom of these intergrading organisms, excluded from more narrowly defined kingdoms of Plantae (Embryophyta) and Animalia (Metazoa). Although only part of the Protista, such as Foraminifera and Radiolaria, have been included customarily in works on invertebrate paleontology, it is proposed to expand the *Treatise on Invertebrate Paleontology* by incorporating all known groups of fossil Protista (diatoms, charophytes, and various other algae).

INTRODUCTION

THE PURPOSE of this paper is to discuss problems of classifying groups of organisms, some of which have been agreed to belong among invertebrate animals, whereas others are accepted as belonging with plants. For example, the Foraminifera and Radiolaria are considered to be animals; these really complex organisms commonly are arranged with sponges, coelenterates, mollusks, and other creatures that ingest solid food and mostly possess the ability to move about freely. They lack powers of photosynthesis which may provide carbohydrates, starch, proteins, and oils from inorganic sources, and they do not have an enclosing wall of cellulose such as the plants characteristically bear. On the other hand, the Myxophyceae (blue-green algae), Chlorophyceae (grass-green algae), and similar organisms which include dendroid growths like the giant kelp, ranging to more than 150 feet in height, are recognized as plants. Using energy from the sun's rays, their contained chlorophyll breaks down carbon dioxide, water, and mineral salts for the manufacture of food that is utilized or stored up in the cells. Some are composed of many cells joined together, living in fixed location or floating inertly in water. Beyond doubt, these organisms differ markedly from typical animals.

If these observations and conclusions are true, how can one encounter any significant problems in classification? Suppose that some groups of organisms, not yet specified here, are found to have characters belonging typically to animals and at the same time other characters belonging typically to plants. Does this discovery invalidate the centuries-long recognized distinction between animals and plants? This can hardly be necessarily so. An agreement by zoologists and botanists to draw an arbitrary line between their respective fields conceivably could lead to general adoption of classification which would allocate some assemblages to the animal side of the staked-out fence and others to the plant side. Thus, we might accept a taxonomic placement of plantlike animals and provide also for recognition of animal-like plants.

An alternative disposition is to segregate organisms having intermediate or intergrading characters, so that artificial separation of them into parcels assigned either to the animal kingdom or the plant kingdom is avoided. Such procedure in classification might well serve to sharpen the fundamental criteria for differentiating animals and plants as restricted by eliminating organisms placed in the newly recognized kingdom, and it might express in far better manner the accumulated evidence concerning the phylogeny of all discovered forms of life on the globe. Clearly, this subject has far-reaching importance. Considering the fact that it is by no means new, prevailing indifference to dealing with it probably is explained by the preoccupation of most botanists and zoologists with other matters, and by compartmentation of scientists

themselves. An easier course is to follow convention, ignoring exceptions to general rule or making qualifications for them so as to dispose of difficulties in one way or another. Then, discordance in classification is an inevitable result.

ORGANISMS VARIOUSLY CLASSED AS ANIMALS OR PLANTS

At least a dozen large assemblages of organisms, mostly unicellular, are classified simultaneously as animals in nearly all zoological works of comprehensive scope and as plants in nearly all botanical references of likewise comprehensive scope. In addition, there are several groups—diatoms, for example—which are assigned by common consent to the plants (although Ehrenberg classed them as true animals) but which seem definitely to belong closely associated with types of organisms claimed to be animals. A main division of the protozoans, called Mastigophora (Diesing, 1865) by most zoologists and variously treated as a

TABLE 1—DIVERGENT CLASSIFICATION OF ORGANIC ASSEMBLAGES[1]
(Phylum—P; Class—C; Order—O; Family—F)

Classification as Plants	Group	Classification as Animals
Chloromonadophyta (P) Chloromonadineae (C) Chloromonadales (O)	Chloromonads	Protozoa (P) Flagellata (C) Chloromonadina (O)
Chrysophyta (P) Chrysophyceae (C) Chrysomonadales (O)	Chrysomonads	Protozoa (P) Flagellata (C) Chrysomonadina (O)
Chrysophyta (P) Chrysophyceae (C) Chrysomonadales (O) Coccolithophoridaceae (F)	Coccolithophorids	Protozoa (P) Flagellata (C) Coccolithophorida (O)
Pyrrophyta (P) Cryptophyceae (C) Cryptomonadales (O)	Cryptomonads	Protozoa (P) Flagellata (C) Cryptomonadina (O)
Pyrrophyta (P) Desmokontae (C) Desmomonadales (O)	Desmomonads	Protozoa (P) Flagellata (C) Peridiniina (O)[2] Desmomonadidae (F)
Pyrrophyta (P) Dinophyceae (C)[3] Dinoflagellata (O)	Dinoflagellates	Protozoa (P) Flagellata (C) Peridiniina (O)[2]
Pyrrophyta (P) Dinophyceae (C)[3] Ebriideae (O)	Ebriids	Protozoa (P) Flagellata (C) Ebriida (O)
Euglenophyta (P) Euglenophyceae (C)	Euglenids	Protozoa (P) Flagellata (C) Euglenoidina (O)
Chlorophyta (P) Chlorophyceae (C) Volvocales (O)	Phytomonads	Protozoa (P) Flagellata (C) Phytomonadina (O)
Chrysophyta (P) Silicoflagellata (C)	Silicoflagellates	Protozoa (P) Flagellata (C) Silicoflagellata (O)
Eumycophyta (P) Myxomycetes (C)	Slime molds	Protozoa (P) Rhizopoda (C) Mycetozoa (O)
Chrysophyta (P) Heterokontae (C) Heterochloridales (O)	Xanthomonads	Protozoa (P) Flagellata (C) Xanthomonadina (O)

[1] In some classifications of Protozoa, the subphylum Plasmodroma is recognized to include the Flagellata (Cohn, 1853) [=Mastigophora Diesing, 1865] and Rhizopoda as classes, and members of the Flagellata are grouped in subclasses called Phytomastigophora and Zoomastigophora. These terms for subphylum and subclasses are omitted in the table.

[2] Peridiniina Ehrenberg, 1830 (as Peridinieae) has priority over Dinoflagellata Bütschli, 1885.

[3] Dinophyceae Pascher, 1914, is a generally recognized name, even though Peridinieae Ehrenberg, 1830, has priority.

subphylum or class, is synonymous with the Flagellata (Cohn, 1853), to which botanists have referred a multitude of chlorophyll-bearing and colorless (partly saprophytic) forms of algae. Fritsch (1935, p. 2), a leading British authority on the algae, points out that "distinction between Algae and Flagellata can no longer be maintained," while in another direction Grassé (1952, p. 39) links the "superclass Flagellata" with rhizopod protozoans (including foraminifers, amoebas, and radiolarians) in a subphylum named Rhizoflagellata. Table 1 sufficiently indicates the divergence in classification and nomenclature of groups which currently are assigned to the animal kingdom and at the same time are included in the plant kingdom.

Another way of making comparison which emphasizes divergence in classification is shown in Table 2. This omits mention of bacteria and groups of algae which are placed by tacit agreement among lowly plants, and it also omits the Sarcodina, Sporozoa, and Ciliophora representing protozoans which are arranged universally as lowly types of animals. Attention is focused on remaining groups of acellular organisms. Nomenclature in the table is uniform in the left- and right-hand columns, corresponding to that given in Table 3, which is based on priority of publication. For classification according to botanists, textbooks by Fritsch (1935) and Smith (1950) are selected as authoritative and representative; similarly, zoological classification is based on selection of recent comprehensive texts by Grassé et al. (1952) and Hall (1953).

TABLE 2.—COMPARISON OF ASSIGNMENTS OF SOME GROUPS OF ACELLULAR ORGANISMS TO PLANTS OR ANIMALS BY BOTANISTS AND ZOOLOGISTS, RESPECTIVELY

(Classification is indicated typographically as follows: *italics* = plants, **boldface** = animals, light-face roman = includes both plants and animals. Enclosure of a name in parentheses denotes omission of mention of the group by either of the two botanical or two zoological works cited, classificatory assignment being then inferential)

Botanical Classification (Fritsch, 1935; Smith, 1950)	Zoological Classification (Grassé et al., 1952; Hall, 1953)
Chlorophyceae	Chlorophyceae
Volvoceae	**Volvoceae**
Tetrasporeae	(*Tetrasporeae*)
Chlorococceae	(*Chlorococceae*)
Ulotricheae	(*Ulotricheae*)
Cladophoreae	(*Cladophoreae*)
Chaetophoreae	(*Chaetophoreae*)
Oedogonieae	(*Oedogonieae*)
Conjugeae	(*Conjugeae*)
Siphoneae	(*Siphoneae*)
Chareae	(*Chareae*)
Chrysophyta	(Chrysophyta)
Heterokontae	Heterokontae
Heterochloridales	**Heterochloridales**
Heterocapsales	**Heterocapsales**[1]
Heterococcales	Heterococcales[2]
Heterotrichales	*Heterotrichales*[3]
Heterosiphonales	(*Heterosiphonales*)
Chrysophyceae	Chrysophyceae[2]
Chrysomonadina	**Chrysomonadina**[1]
Rhizochrysidales	**Rhizochrysidales**
Chrysocapsales	**Chrysocapsales**
Chrysotrichales	*Chrysotrichales*[3]
Chrysosphaerales	(*Chrysosphaerales*)
Coccolithophorida	**Coccolithophorida**
Silicoflagellata	**Silicoflagellata**
Diatomacea	(*Diatomacea*)
Pyrrophyta[4]	**(Pyrrophyta)**
Peridinieae	**Peridinieae**
Dinocapseae	**Dinocapseae**
Dinococceae	**Dinococceae**
Dinotricheae	**Dinotricheae**[2]
(Ebriacea)	**Ebriacea**[2]
Desmokontae	**Desmokontae**[2]
Euglenoidina	**Euglenoidina**
Chloromonadina	**Chloromonadina**
Cryptomonadina	**Cryptomonadina**
(*Myxomycetes*)	**Myxomycetes**

[1] Omitted by Grassé et al.
[2] Omitted by Hall.
[3] Grassé et al. include some plants.
[4] Omitted by Fritsch.

KINGDOM PROTISTA

The concept that living things may be divided rationally into more than two kingdoms, consisting of the Plantae and Animalia, is roughly half as old as the date of beginning recognized botanical nomenclature (1753, Linné's *Species Plantarum*, 1st. ed.) and recognized zoological nomenclature (1758, Linné's *Systema Naturae*, 10th ed.). Hogg, in 1860, proposed the removal of various organisms that are not clearly classifiable as either plants or animals, segregating them in an independent biological division which he named Protoctista (Greek, *protos-ctistos*, first established or created). Haeckel (1866), with the same objective, later published the term Protista (Greek, *protista*, very first) which has gained currency by establishment of the journal *Pro-*

tistenkunde and by reference to it in many textbooks, even though it has not been adopted generally in classification of organisms. Copeland (1938) adopted Protista as the name for a separate kingdom composed of mainly unicellular nucleate organisms but later (Copeland, 1947) he called attention to Hogg's proposal of Protoctista and accepted this term instead of Protista. Grassé (1952), in a recently published volume of the great *Traité de Zoologie*, recognizes the kingdom ("grand phylum") Protista, considering it to be composed of two phyla (embrachements), Protophyta and Protozoa, but only the protozoans are described. These include all of the organisms listed in Table 1 of the present paper. Such definition of Protista is essentially meaningless because the old, arbitrary boundary between plants and animals persists, being simply moved over to a position that takes from the botanists all that zoologists can claim.

Although one always must remember that the discovered forms of life on the earth are parts of a very incompletely known continuum in which many closely similar segments denote convergence in evolution, rather than near relationship, trustworthy taxonomic arrangement of the observed kinds of living and extinct organisms is not a remotely unattainable goal. Advancement toward it proceeds in many areas year after year. Whenever and wherever some of the man-made walls, shelves, bins, and pigeonholes are found to be ill-suited for "natural" sorting of the organic world, the removal or addition of partitions and changes in magnitude of filing compartments may be required. Forcible placement of objects where they do not fit is unallowable, either on the ground of ignorance or on the basis of unwillingness to remodel the receiving spaces. A system that promotes filing the same thing by different clerks in different places or that calls for erratic breaking apart of units so as to permit storage in widely separated sections of a warehouse must be faulty. These are pertinent thoughts bearing on the proposal to recognize a kingdom called Protista.

Scope of the Protista

What groups of organisms are better classed in the kingdom Protista than held as members of the plant and animal kingdoms? Answer to this question depends primarily on how we define these three main divisions and secondarily on how accurately and completely we understand the many forms of life which are to be classified. The lines of demarcation between respective kingdoms should be so drawn that they are not only recognized easily but accepted for outlining most significant main groups which have attributes of evolution in common.

A valid approach to this problem is offered by study of the nature of cellular organization. Very briefly and simply, the Protista may be defined to include all acellular organisms, that is those possessing within a single cell total properties of life which may reproduce itself; the body does not require an organized arrangement of differentiated, mutually interdependent cells. This is a workable and meaningful definition, for it brings together the host of least complexly built forms of life which have intergrading characters commonly associated with attributes of plants on the one hand and with peculiarities of animals on the other. A vast number of these acellular organisms persist throughout their existence as isolated single cells; they are unicellular as well as acellular. Many others grow together in colonies, among some of which there is even an appreciable degree of functional differentiation, and it is a convenient common practice to call such assemblages multicellular, in spite of the fundamentally acellular nature of the organic structure which is shown by the invariably acellular nature of the reproductive unit.

Members of the Plantae (Embryophyta) and Animalia (Metazoa), restricted by exclusion of acellular organisms now placed in the Protista, are distinguished by their universally multicellular organization, with differentiation of functions among parts of such sort that the individual cells are interdependent. Isolated cells cannot survive and reproductive mechanisms are specialized. The differences between plants and animals defined in this way is profound. Unquestionably, such plants and animals are divergent evolutionary products of protistan ancestors.

Without much doubt, an important reason for tardy recognition of the Protista as

a very significant division of the organic world is faultiness in defining the scope of protistans. Because this stems from Haeckel's exclusion of many algae and the fungi, although he included diatoms and a host of unicellular algae, one might challenge adoption of the name Protista, especially when it is discovered that Haeckel considered sponges to belong in this assemblage. The availability of any given name, such as Protista, and its usefulness depend more on application which comes to be accepted than on originally published concepts. Therefore, we may inquire about appropriateness of the term in different senses.

A prevailing idea with respect to protistans has been that they are exclusively unicellular (rather than acellular). Thus Carter (1951, p. 23) writes:

> The distinction between the single-celled plants (Protophyta) and animals (Protozoa) is one which it is difficult to make logical. It is often said that all organisms containing chlorophyll are plants. Single-celled organisms containing chlorophyll are therefore called Protophyta and the many closely related forms which are without chlorophyll are also frequently included in the Protophyta, for not all plants contain chlorophyll. But the organization of these forms is very like that of many which are usually grouped as Protozoa. It is difficult to believe that the distinction is a natural one. It seems better for our purposes to use the term Protista for all single-celled organisms which have the complete organization of the cell. Thus we shall avoid the necessity of distinguishing the Protophyta and Protozoa.

Grassé et al. (1952) include many multicelled (colonial) organisms in the Protista but in various places refer to evolution in the direction of the "true algae," which are excluded from consideration as protistans. Jahn & Jahn (1949), on the other hand, regard protistans as including the green, red, and brown algae, which comprise many large dendroid multicelled growths, along with the Protozoa, and they assign to the Monera (classed in this paper as a division of the Protista) the blue-green algae, bacteria, and spirochaetes. Fritsch (1935), Smith (1950, 1951), and others have made very clear that no valid separation can be made between unicellular organisms classed as algae (or as protozoans by most zoologists) and so-called multicellular "true algae."

We may conclude that a definition of Protista which restricts application of the name to unicellular organisms, rather than to acellular ones, and which does not incorporate algal growths formed of many cells joined together is quite as unacceptable as arbitrary classification of these organisms among plants or animals. The multicellular algae retain acellular fundamental attributes.

Classification

The acellular organisms grouped together in the Protista are divisible into two fairly distinct assemblages, in both of which there are forms having plantlike and animal-like characters. One division, which must be considered more primitive, is distinguished by the lack of a well-organized nucleus in the cell, even though some exhibit chromatin bodies that may represent a very simple type of nucleus. The bacteria (Schizomycetes), including spirochaetes, and blue-green algae (Myxophyceae) belong here. Collectively, they may be designated as a subkingdom called the Monera (Haeckel, 1866). The other division is characterized by the presence of distinct nuclei in the cells and for it the subkingdom name Protoctista (Hogg, 1860) may be employed. This group includes most of the algae (Myxophyceae excluded), a large number of unicellular flagellates, protozoans, slime molds, fungi, and lichens.

The name Monera was published by Copeland (1938) with application identical to that indicated in this paper but with rank of an independent kingdom. Actually, the distinction between Monera and Protoctista hardly justifies assignment of them to separate kingdoms because recent studies show that rudimentary sorts of nuclei at least are recognizable both in bacteria (Breed, Murray & Hitchens, 1948, p. 65) and blue-green algae (Droute, 1952, p. 159). Copeland's (1947) subsequent substitution of Mychota (Enderlein, 1917), a synonym of Schizomycetes, for Monera is based on misapprehension and on other grounds it is not acceptable.

The definition of Protoctista given by Copeland (1947) and the range of organisms assigned to it by him also agree with statements given in the present paper, but the division is classed here as a subkingdom in-

stead of a kingdom. Copeland's earlier (1938) discussion employed the name Protista for the nucleate acellular organisms (excluding Monera), despite the fact that Haeckel (1866) clearly included the Monera under Protista.

An outline of classification which present knowledge suggests to be best suited for the Protista is given in Table 3. Groups containing fossil representatives are marked by an asterisk (*) and the known stratigraphic range for these is given. Most subdivisions of subordinate rank are omitted.

For comparison with classification of the Protista, a very incomplete statement of some main divisions of the plant and animal kingdoms is given in Table 4.

Nomenclature of Protista

It is evident that if many organisms of acellular nature which previously have been classified as plants, animals, or both plants and animals are transferred to an independent kingdom composed of "plant-animals" or living things which are simply termed organisms, established nomenclature (in so far as one can recognize it) derives from botanical and zoological sources. In general, only botanists have been concerned with nomenclature applied to Rhodophyceae (red algae), for example, and only zoologists have given attention to names for rhizopod and ciliate protozoans. Two sets of conflicting names, however, are applied to several large groups, depending on whether the organisms are arranged in divisions considered to be plants or assigned to divisions considered to be animals (Table 1). What names are most appropriate for protistans? Of course, no International Rules of Protistan Nomenclature exist, and therefore it is pertinent to inquire as to how we may proceed in matters of determining scientific names after a declaration of independence from the two mother kingdoms of Plantae and Animalia has been signed.

Can names which are firmly fixed or reasonably well established in botanical nomenclature on the one hand and in zoological nomenclature on the other be adopted without change, being fitted together smoothly? Perhaps some minor alterations, as in the nature of endings for various taxonomic categories, may aid amalgamation. An investigation is needed to see what material differences, if any, set botanical and zoological nomenclature apart. In addition, one should not overlook viewpoints of successive International Microbiological Congresses concerning the nomenclature of Protista. The first such congress (Paris, 1930) established a permanent committee on nomenclature which has served to guide actions at later triennial meetings of the microbiologists.

A careful reading of all internationally agreed articles relating to the classification and application of names to organisms which may be included in the Protista reveals very few noteworthy conflicts. That officially recognized names for plants and animals are limited by slightly different initial dates (1753, 1758) of works by Linné is quite unimportant, and the fact that the botanical rules specify use of the term "division" (instead of phylum) for a taxonomic category having higher rank than class can be ignored. Zoologists are intrenched in using "phylum." Differences of this sort should not give difficulty.

The botanical and zoological rules allow duplication of names in the sense that no name applied to a plant is excluded from valid application also to an animal, and vice versa. Even though it is extremely hard to find examples of identical names for plants and animals, it is obvious that if different protistans are found to bear the same designation, they must be regarded as homonyms and only the first-published name should prevail. The international microbiological committee recognized this by adopting rules as follows (Breed, Murray, & Hitchens, 1948, p. 63):

> "a. Generic homonyms are not permitted in the group Protista.
> b. It is advisable to avoid homonyms amongst Protista on the one hand, and a plant or animal on the other."

Stipulations of the botanical rules as to endings required for suprageneric taxonomic categories differ from those prescribed by the zoological rules, although the latter refer only to names for families and subfamilies. The divergence and (largely accidental) convergence of usage in choosing the endings of names applied to suprageneric ranks of plants and animals, as shown by a somewhat hasty survey of standard works, is given in

TABLE 3—CLASSIFICATION OF PROTISTA

*PROTISTA Haeckel, 1866 (kingdom), acellular organisms. Precam.-Rec.
*MONERA Haeckel, 1866 (subkingdom), cells lacking a definitely organized nucleus. Precam.-Rec.
*SCHIZOMYCETES Nägeli, 1857 [=Bacteria Cohn, 1872; Schizomycetaceae De Toni & Trevisan, 1889; Bacteriales Clements, 1909; Schizomycetacea Castellani & Chalmers, 1919; Mychota Enderlein, 1924; Schizomycetae Stanier & Van Niel, 1941; Schizomycophyta Tippo, 1942] (phylum). Bacteria. Precam.-Rec.
*MYXOPHYCEAE Stizenberger, 1860 [=Algae Linné, 1753 (partim); Cyanophyceae Sachs, 1874; Schizophyta Cohn, 1875; Schizophyceae Cohn, 1879; Archephyta Jaekel, 1894; Cyanophyta Pascher, 1914; Cyanophycophyta Papenfuss, 1946] (phylum). Blue-green algae. Precam.-Rec.
*SPONGIOSTROMATA Pia, 1928 (class). Precam.-Rec.
*POROSTROMATA Pia, 1928 (class). Cam.-Pleisto.
*PROTOCTISTA Hogg, 1861 (subkingdom), cells with distinct nucleus. ?Cam., Ord.-Rec.
*CHLOROPHYCEAE Kützing, 1845 [=Chlorospermeae Harvey, 1836; Thallophyta Unger, 1838 (partim); Flagellata Cohn, 1853 (partim); Chlorophyllaceae Rabenhorst, 1863: Chlorophyllophyceae Rabenhorst, 1865; Mastigophora Diesing, 1865 (partim); Phytomastigina Doflein, 1901 (partim); Chlorophyta Wettstein, 1901; Phytomastigophora Calkins, 1909 (partim); Chlorophycophyta Papenfuss, 1946; Rhizoflagellata Grassé, 1952 (partim)] (phylum). Grass-green algae. Ord.-Rec.
*VOLVOCEAE Francé, 1894 (as Volvocales) [=Phytomonadina Blochmann, 1895] (class). Eoc.-Rec.
*SIPHONEAE Munier-Chalmas, 1877 [=Siphonocladiaceae Schmitz, 1879] (class). Ord. Rec.
*CHAREAE Nägeli, 1860 (as Characeae) [=Charophyta Graves & Webster, 1920; Charales Lindenbein, 1927] (class). Dev.-Rec.
TETRASPOREAE, CHLOROCOCCEAE, ULOTRICHEAE, CLADOPHOREAE, OEDOGONIEAE, CONJUGEAE (classes). Rec.
*CHRYSOPHYTA Pascher, 1914 [=Thallophyta Unger, 1838 (partim); Phytomastigina Doflein, 1901 (partim); Phytomastigophora Calkins, 1909 (partim); Chrysophycophyta Papenfuss, 1946] (phylum). ?Cam.-Trias., Jur.-Rec.
HETEROKONTAE Luther, 1899 [=Xanthophyceae Pascher, 1913; Xanthomonadina Deflandre, 1952] (class). Rec.
HETEROCHLORIDALES, HETEROCAPSALES, HETEROCOCCALES, HETEROTRICHALES, HETEROSIPHONALES (orders). Rec.
*CHRYSOPHYCEAE Pascher, 1914 (class). U. Cret.-Rec.
*CHRYSOMONADINA Stein, 1878 [=Chrysomonadales Pascher, 1921] (order). U. Cret.-Rec.
RHIZOCHRYSIDALES, CHRYSOCAPSALES, CHRYSOTRICHALES, CHRYSOSPHAERALES (orders). Rec.
*COCCOLITHOPHORIDA Lohmann, 1902 (as Coccolithophoridae) [=Coccolithineae Schiller, 1930; Coccolithophoraceae, Fritsch, 1935] (class). Jur.-Rec.
*SILICOFLAGELLATA Borgert, 1891 (class). U. Cret.-Rec.
*DIATOMACEA Agardh, 1824 [=Diatomeae Haeckel, 1866; Bacillariaceae Pfitzer, 1869; Bacillariales Schütt, 1896; Bacillariophyceae Pascher, 1914] (class). ?Penn., Trias., Jur.-Rec.
*PYRROPHYTA Pascher, 1914 (phylum). ?Penn., Jur.-Rec.
*PERIDINIEAE Ehrenberg, 1830 [=Dinoflagellata Bütschli, 1885; Peridiniales Schütt 1896; Dinophyceae Pascher, 1914] (class). ? Penn., Jur.-Rec.
DINOCAPSEAE, DINOCOCCEAE, DINOTRICHEAE (classes) Rec.
*EBRIACEA Lemmermann, 1900 (as Ebriaceae) [=Ebriideae Deflandre, 1936] (class). Paleoc.-Rec.
DESMOKONTAE Pascher, 1914 (class). Rec.
*EUGLENOIDINA Bütschli, 1884 [=Euglenida Blochmann, 1895; Euglenophyceae, Euglenophyta Pascher, 1931; Euglenineae Fritsch, 1935] (phylum). Eoc.-Rec.
CHLOROMONADINA Klebs, 1892 [=Chloromonadophyta Prescott, 1950] (phylum). Rec.
CRYPTOMONADINA Ehrenberg, 1832 [=Cryptophyceae Pascher, 1914] (phylum). Rec.
EUFLAGELLATA Claus, 1887 [=Zoomastigina Doflein, 1901; Zoomastigophora Calkins, 1909; Zoomastigoda Calkins, 1926] (phylum). Rec.
*RHODOPHYCEAE Ruprecht, 1855 [=Rhodospermeae Harvey, 1836; Rhodophyta Pascher, 1914; Rhodophycophyta Papenfuss, 1946] (phylum). Red algae. Ord.-Rec.
PHAEOPHYCEAE Kjellman, 1891 [=Rhodospermeae Harvey, 1836; Thallophyta Unger, 1838 (partim); Phaeophyta Pascher, 1914; Phaeophycophyta Papenfuss, 1946] (phylum). Brown algae. Rec.
MYXOMYCETES Wallroth, 1833 [=Mycetozoa de Bary, 1858] (phylum). Slime molds. Rec.
*EUMYCOPHYTA Tippo, 1942 (phylum). Fungi. Dev. -Rec.
*PROTOZOA Goldfuss, 1818 (phylum). Cam.-Rec.
*SARCODINA Hertwig & Lesser, 1874 [=Rhizoflagellata Grassé, 1952 (partim)] (subphylum). Cam.-Rec.
*RHIZOPODA Dujardin, 1841 (class). ?Cam., Ord.-Rec.
AMOEBAEA Ehrenberg, 1830 [=Gymnamoeba Haeckel, 1862; Amoebida Claparéde & Lachmann, 1858; Amoebina Cash & Hopkinson, 1905] (subclass). Rec.

PROTEOMYXA Lankester, 1885 (subclass). Rec.
*THALAMIA Haeckel, 1862 [=Testacea Schultze, 1884; Testaceafilosa, Testacealobosa de Saedeleer, 1934; Thecamoebidae Schaeffer, 1926] (subclass). Eoc.-Rec.
*FORAMINIFERA d'Orbigny, 1826 (subclass). ?Cam., Ord.-Rec.
*ACTINOPODA Calkins, 1909 (class). Cam.-Rec.
HELIOZOA Haeckel, 1866 (subclass). Rec.
*RADIOLARIA Müller, 1858 (subclass). Cam.-Rec.
SPOROZOA Leuckart, 1879 (subphylum). Rec.
*CILIOPHORA Doflein, 1901 (subphylum). Jur.-Rec.
*CILIATA Perty, 1852 (class). Jur.-Rec.
PROTOCILIATA Metcalf, 1918 (subclass). Rec.
*EUCILIATA Metcalf, 1918 (subclass). Jur.-Rec.
*SPIROTRICHIDA Bütschli, 1889 (order). Jur.-Rec.
*TINTINNINA Claparéde & Lachmann, 1858 (suborder). Jur.-Rec.
HETEROTRICHINA, OLIGOTRICHINA, ENTODINIOMORPHINA, HYPOTRICHINA (suborders). Rec.
HOLOTRICHIDA, PERITRICHIDA, CHONOTRICHIDA (orders).
SUCTORIA Claparéde & Lachmann, 1858 (class). Rec.

TABLE 4—SOME DIVISIONS OF THE PLANT AND ANIMAL KINGDOMS

*PLANTAE Linné, 1753 (kingdom). Dev.-Rec.
*BRYOPHYTA Eichler, 1886 (phylum). Penn.-Rec.
*PTERIDOPHYTA Eichler, 1886 (phylum). Dev.-Rec.
*SPERMATOPHYTA Eichler, 1886 (phylum). Dev.-Rec.
*ANIMALIA Linné, 1758 (kingdom) [=Metazoa, Haeckel, 1874]. Precam.-Rec.
AGNOTOZOA Moore, Lalicker, & Fischer, 1953 (subkingdom). Rec.
MESOZOA Kukenthal & Krambach, 1923 (phylum). Rec.
*PARAZOA Sollas, 1884 (subkingdom). Cam.-Rec.
*ARCHAEOCYATHA Vologdin, 1937 [=Pleospongia Okulitch, 1940] (phylum). L. Cam.
*PORIFERA Grant, 1836 [=Spongiaria de Blainville, 1816; Spongiae Haeckel, 1866] (phylum). Cam.-Rec.
*EUMETAZOA Kukenthal & Krumbach, 1923 (subkingdom). Cam.-Rec.
*COELENTERATA Leuckart, 1847 [=Cnidaria Hatschek, 1888] (phylum). Cam.-Rec.
Other phyla.

Table 5. The italicized endings are those explicitly called for by the rules; an asterisk (*) indicates recommendation by the international rules but not prescription.

It is evident from inspection of the tabulated endings that "almost anything goes." In botany, the range of variation is notably smaller than in zoology but use of the termination -eae (specified for tribe), for example, is extended to class, subclass, and suborder; on the other hand, orders are very consistently marked by the ending -ales. Only a single conflict between endings required by the botanical and zoological rules exists as they now stand; this is in application of -inae, which is abundantly used for subfamilies in zoology and rarely used for subtribes in botany. If any subtribes need to be recognized among protistans (none now are known), an ending other than -inae should be chosen. Otherwise, nomenclature already established for suprageneric categories may be considered admissible in the kingdom Protista, for it really makes no difference at

TABLE 5.—ENDINGS FOR SUPRAGENERIC TAXONOMIC CATEGORIES OF PLANTS AND ANIMALS

Plants	Category	Animals
-a	Phylum (division)	-a, -ea
-ida	Subphylum	-a
-eae, -es	Class	-a, -ae, -ea, -es, -ida, -idea
-ae, -eae, -ideae, -oideae	Subclass	-a, -ata, -es, -ea, -i, -ia, -ida, -idia, -ina
*-ales, -ata	Order	-a, -ae, -acea, -aria, -ata, -ea, -i, -ia, -ida, -idea, -iformes, -ina, -oidina
-atae, -eae, -ineae, -oideae	Suborder	-a, -aria, ata, -ea, -ia, -ina, -ites, -oidea
-oideae	Superfamily	-a, -acea, -aceae, -icae, -ida, -oida, -oidae
-aceae	Family	*-idae*
-oideae, -ideae	Subfamily	*-inae*
-eae, -ae	Tribe	-ae, -i, -ites, -ides
-inae	Subtribe	

all if some families bear the ending -idae while others have -aceae; likewise, subfamilies with the ending -inae may without harm show trace of their zoological affinities while those in other groups by retaining -oideae indicate nomenclature originally under the botanical rules. This seems to be a rational procedure that has the virtue of avoiding nomenclatural disturbance.

Special consideration must be given to the problem of deciding on what suprageneric names should take precedence in the case of assemblages that have been classified as plants by botanists and as animals by zoologists. This affects groups listed in Table 1. A logical solution is to recognize the first-published name, making change only in the ending where this is needed to take account of altered assignment of taxonomic rank. For example, the name Coccolithophorida for a class may be substituted for the originally published Coccolithophoridae Lohmann, 1902 (family). Also, the class name Volvoceae may replace the ordinal name Volvocales Francé, 1894, and take precedence over Phytomanadina Blochmann, 1895, which was applied to the same group. These principles have guided preparation of the outline of classification of the Protista given in Table 3.

Now we come to another rather important difference between the botanical and zoological rules. This is the provision (Botanical Rules, Art. 38) that, except as applied to bacteria, no name published after 1934 as designation of a plant shall be recognized as valid unless it is accompanied by a Latin diagnosis. No such rule exists or seems to have been proposed for the naming of animals. It should be rejected for all Protista and not merely for bacteria.

STATUS OF PROTISTA IN THE TREATISE ON INVERTEBRATE PALEONTOLOGY

The first-made plans for the *Treatise on Invertebrate Paleontology*, sponsored by the Paleontological Society, Society of Economic Paleontologists and Mineralogists, and Geological Society of America on the west side of the Atlantic, and by the Palaeontographical Society in Great Britain, called for preparation of a series of volumes dealing with each of the well-recognized phyla of invertebrate animals which are represented by fossils. The Protozoa were listed as one of these. The fact that protozoans are considered by many zoologists to constitute a subkingdom, correlative in rank with Metazoa, did not affect the program of organizing the *Treatise*. Also, vague grouping of protozoans with low orders of plants was given scant attention. Subsequently, the anomalies encountered in trying to define exactly the scope of Protozoa has led me, as editor of the *Treatise*, to modify the outline for initial volumes of this work in manner likely to be considered heterodox by many paleontologists and other biologists. In a word, it is proposed to recognize Protista as a separate kingdom and to include description of known fossil representatives of all kinds—not merely those classed as Protozoa. This decision accounts for preparation of the present paper.

The arguments which favor segregation of the Protista as an organic assemblage correlative in rank with the plant and animal kingdoms, each restricted, gain strength from year to year as knowledge and understanding advance. They are incompletely and inadequately presented in this short paper, and therefore it is pertinent to report that consultation with specialists on various groups of protistan organisms (bacteria, algae, and protozoans) has helped greatly to confirm my own conclusions, rather than to overthrow them. It seems logical to extend a study of protozoans by surveying other acellular organisms that have characters intergrading with them; it seems illogical to respect a false and instable boundary between acellular plants and animals—false because it is unnatural, instable because it is shifted back and forth according to botanical or zoological viewpoints. The problem of planning this part of the *Treatise* is satisfactorily solved.

What about the objection that bacteria, for example, are not invertebrates? What justification can be offered for including calcareous algae and diatoms in a textbook on invertebrate paleontology? To be sure, these organisms lack vertebrae and in varying degree they engage the labors of paleontologists, but it is necessary to confess that heretofore only part of protistan paleontology ordinarily has been put in the domain of invertebrate paleontology, or as some would

say, invertebrate paleozoology. One must agree that study of fossil Protista belongs to paleontology, for as a whole it can be neither paleobotany nor paleozoology. Accordingly, if some insist that the title of the *Treatise* is made a misnomer by including organisms previously classed generally as lowly plants, they have their point; the title became fixed before the scope of the *Treatise* was expanded. The intention to provide descriptions of conodonts and problematical fossils in Part W may already have invalidated precise correspondence of the *Treatise* with its title.

Finally, it is worth remembering that it is those who call themselves invertebrate paleontologists (including micropaleontologists) who are chiefly busy with Protista, conodonts, and the like. Paleobotanists and vertebrate paleontologists are concerned almost exclusively with other things. Therefore, practical convenience is a consideration having merit as added support for inclusion of all Protista in the *Treatise*.

CONCLUSIONS

1. Various groups of acellular organisms which are classed as animals (protozoans) by zoologists and at the same time as plants (protophytes) by botanists, actually intergrade in characters with one another and with assemblages such as the bacteria, algae, fungi, slime molds, and all types of protozoans. Comparative study of them indicates that the importance of their interrelationships greatly outweighs differences which have led to traditional classification of some as lowly plants and others as lowly animals. The boundary between such groups is tenuous, artificial, and instable.

2. Advances in knowledge, especially in recent decades, furnish ever-increasing support to classification proposed approximately a century ago, that these acellular organisms should be assigned to an independent kingdom and that the plant and animal kingdoms should be restricted by excluding the acellular organisms.

3. The name Protista is the most suitable one for the kingdom of acellular organisms, particularly on the grounds of its expanding (although yet very limited) usage.

4. Protistans are divisible into two subkingdoms: Monera, comprising organisms that lack a definitely developed nucleus in the cell (bacteria, bluegreen algae); and Protoctista, in which the cells have a distinct nucleus (other algae, many flagellate organisms, fungi, protozoans).

5. Nomenclature of the Protista is cared for readily by applying the mostly accordant provisions of the international botanical and zoological rules, but duplication of names (homonyms) introduced by transfer of them from other kingdoms cannot be allowed. Also, some deviation from stipulations as to endings for suprageneric categories needs to be permitted. Otherwise, nearly all existing names can be recognized without alteration. Where botanical names and zoological names have been given to the same group of organisms, the oldest one should prevail. The requirement of a Latin diagnosis for names introduced since 1934, adopted for botanical names, is not acceptable for protistan nomenclature.

6. Plans for the *Treatise on Invertebrate Paleontology* have been changed so as to provide for inclusion of descriptions of all protistan groups represented by fossils.

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PHYLOGENY OF THE CAMBRIAN TRILOBITE FAMILY CATILLICEPHALIDAE AND THE ONTOGENY OF *WELLERASPIS*

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ABSTRACT—The genera *Lonchocephalus* and *Welleraspis*, provisionally assigned to the family Solenopleuridae, and the genera *Buttsia*, *Catillicephala*, *Distazeris*, *Madarocephalus*, *Pemphigaspis*, *Stenochilina*, *Theodenisia* and *Triarthropsis*, assigned to the family Catillicephalidae, are redescribed and illustrated. An almost unbroken series of intermediate forms indicates that such specialized genera as *Catillicephala* and *Theodenisia*, notwithstanding their superficial corynexochid aspect, are of almost certain ptychopariid descent, and that their immediate ancestors were genera similar to *Lonchocephalus* and *Welleraspis*, common in the late Medial Cambrian of North America. A series of ontogenetic stages, from the metaprotaspis to the adult, is described for the species *Welleraspis swartzi* (Tasch). The cephalic characters of the meraspis are similar to those assumed by some of the later forms (*Theodenisia*).

INTRODUCTION

THE PURPOSE of this paper is to present the phylogenetic and taxonomic conclusions reached by the writer from the study of a group of genera of Upper Cambrian trilobites, here assigned to the families Solenopleuridae and Catillicephalidae.

Of the trilobites of all ages, the Late Cambrian ones are those whose taxonomy is in the state of greatest confusion. The Late Cambrian epoch witnessed an extensive diversification of the trilobites, in contrast to the relatively small number of types present in the Early Cambrian and most of the Medial Cambrian. Distant lineages developed superficially similar forms, while closely related genera sometimes assumed greatly different aspects. Eventually, through the poorly known stages of trilobite evolution that took place in the Early Ordovician, there became established the readily recognizable families that represent the class through its remaining life span from the Medial Ordovician to the Permian. Hence, understanding the phylogenetic relations among Upper Cambrian trilobites and the derivation of the Ordovician families from them, is one of the main problems for the trilobite taxonomist.

The writer believes that, within a small group of trilobites, some progress has been made through the study here presented. The relationship of a number of genera, some of which at first sight look so different that they had so far been considered unrelated, has been made probable by tracing almost unbroken series of intermediate form, continuous not only morphologically but also chronologically. Facts concerning the phylogenetic and taxonomic value of various characters of the trilobite exoskeleton have emerged, and may help to work out the phylogeny of other groups. Finally, the finding of an almost complete ontogenetic series for one of the genera here discussed, induced the writer to describe and figure these larval forms, since ontogeny may have some bearing on the phylogeny.

The plan of this paper is as follows: First, the genera on which the discussion is mainly based are redescribed, using both published and new observations. Drawings illustrating the known parts of the exoskeleton for all of these genera are presented, since they show the diagnostic features much better than photographs of specimens.* Nomenclatural questions are treated only incidentally. The second section of the paper describes the ontogeny of *Welleraspis*. The third section discusses the relationships

* These drawings were prepared by the writer by tracing the outlines from large prints of original photographs, hence the proportions are rigorously accurate. Figure 1 is after Palmer (1951); figure 2c after Wilson (1951).

among the described genera and suggests possible ancestors.

SYSTEMATIC DESCRIPTIONS

Superfamily PTYCHOPARIACEA
Family ?SOLENOPLEURIDAE Angelin, 1854

The less specialized forms here discussed are provisionally assigned to the family Solenopleuridae, founded on a genus from the Middle Cambrian of the Acado-Baltic province. It has been customary to refer genera like *Lonchocephalus* and *Welleraspis* to the Solenopleuridae; this is, for instance, the classification adopted by Kobayashi (1935). Most of the known morphological features (excepting the number of thoracic segments and the size of the pygidium) are similar to those of the type genus. On the other hand, Resser excluded from the family all genera not occurring in the Acado-Baltic province, presumably on the ground that since trilobites from the Acado-Baltic province on one side, and the Appalachian, Central and Cordilleran provinces on the other side, were separated from each other by some kind of barrier during the entire Medial and Late Cambrian epochs, similar forms occurring in the two areas were not likely to possess near common ancestor, but should rather be interpreted as parallel developments in distantly related stocks. In principle, the argument may be sound, and the writer concurs in preferring a phylogenetic classification to one based on superficial similarities. However, at the present stage of knowledge of the Cambrian trilobites, a phylogenetic classification of the host of Cambrian ptychopariid and solenopleurid genera is out of the question. Almost identical forms occur in Cambrian deposits all over the world, and it would appear unjustified to refuse to admit North American trilobites in the families Ptychopariidae and Solenopleuridae on purely paleogeographic grounds.

It is possible that some day an unbroken lineage will be found, leading from North American Middle Cambrian ptychopariids to *Lonchocephalus* and *Welleraspis*. At that time, it will become opportune to switch from a "horizontal" to a "vertical" classification, placing these genera, with some of their ancestors and possibly descendants, in a phylogenetic family where wider morphologic diversity is allowed. In a later section, suggestions about such possible ancestry are made; however, they do not at present appear sufficiently well substantiated to supply a basis for classification. In the meantime, it seems expedient to assemble morphologically similar genera in such conventional families as the Ptychopariidae and Solenopleuridae as construed by most authors.

As it will be shown in this paper, it seems very likely that solenopleurid genera similar to *Welleraspis* rapidly evolved into highly specialized forms, like *Catillicephala*, which have lost most of the characteristic features of their ptychopariid ancestors. Then the question arises: Where should one place the boundary between the Solenopleuridae (or whatever family is to include *Lonchocephalus* and *Welleraspis*) and the Catillicephalidae? The author decided to place this dividing line between *Welleraspis* and *Distazeris*, where at present there seems to be a somewhat wider morphological gap than between any other two of the genera in question. It is obvious that further discoveries may fill this gap as well as others.

Genus LONCHOCEPHALUS Owen, 1852
Text-figure 1a

Trilobites of small size. Glabella subovate, somewhat tapered forward, rounded in front, defined all around by a deep dorsal furrow. Glabellar furrows usually well impressed, curving inward and backward, especially the posterior pair that almost isolate basal lobes. Occipital furrow deep, occipital ring usually extended into a long spine. Frontal limb well developed, divided into brim and border by a well-marked marginal furrow. Fixed cheeks convex, downsloping, less than half as wide as the glabella at the palpebral lobes. Ocular ridges distinct, palpebral lobes narrow, less that one-fourth the glabellar length, at level of glabellar midpoint. Posterior marginal furrow deep. Anterior facial sutures directed forward in front of eyes, gradually curving inward, marginal for some distance near midline. Posterior branch almost straight for a distance behind the eyes, curving inward and rounding off posterior angles of cranidium. Free cheeks with genal spines.

Thorax of seven segments (*L. chippewaen-*

sis). Pygidium transversely subtriangular, with prominent, conical, well-segmented axis reaching posterior margin. Pleural lobes flat; pleural furrows impressed, marginal furrow weak or obsolete. In type species, margin sharply downfolded to form almost vertical slope.

Type species.—*Lonchocephalus chippewaensis* Owen, 1852 (designated by Miller, 1889).

Stratigraphic and geographic range.—Dresbachian of Appalachian, Central and Cordilleran provinces of North America.

Remarks.—Of the genera discussed in this paper, *Lonchocephalus* is the least specialized, still preserving the cephalic appearance of the generalized ptychopariids common in Lower and Middle Cambrian strata. The type species is illustrated in figure 1a.

Species assigned to the genus.—The following species are placed in *Lonchocephalus*. Some of them intergrade with *Welleraspis* (e.g. *L. plenus*, *L. verrucosus*). No careful study of possible synonymies was made.

Lonchocephalus chippewaensis Owen, 1852
Conocephalites minutus Bradley, 1860
C. minor Shumard, 1863
C. verrucosus Whitfield, 1884
Lonchocephalus bunus Walcott, 1916
L. pholus Walcott, 1916
L. montanensis Lochman, 1944

Genus WELLERASPIS Kobayashi, 1935
Text-figures 1b-c; 4a-c

Trilobites of small size. Cranidium similar to *Lonchocephalus*, with proportionately larger glabella of subquadrate shape. Frontal limb shorter (sag.). Palpebral lobes somewhat anterior to glabellar midpoint. Free cheeks with very short genal spines. Doublures of free cheeks separated by rostrum (*W. swartzi*). Hypostoma with angular anterior outline, well rounded posteriorly, with a continuous marginal furrow and narrow border. A pair of deep lateral depressions extend inward and backward, becoming shallower without quite meeting on midline.

Pygidium with prominent, conical, well-segmented axis almost reaching posterior margin. Pleural lobes furrowed, downsloping, with flat border defined by shallow marginal furrow.

Type species.—*Solenopleura jerseyensis* Weller, 1899.

Synonym.—*Avonaspis* Lochman, 1940 (type: *Avonaspis missouriensis* Lochman) is considered a subjective synonym.

Stratigraphic and geographic range.—Dresbachian of the Appalachian, Central, and possibly Cordilleran provinces of North America.

Remarks.—*Welleraspis* is slightly more specialized than *Lonchocephalus* in possessing a larger, untapered glabella, and constitutes a transition to the following genus, *Distazeris*. The type and another species are illustrated in figures 1b, 1c.

Species assigned to the genus.—No careful study of possible synonymies among the listed species was made.

Solenopleura jerseyensis Weller, 1899
Stenochilina anceps Resser, 1938
S. appalachia Resser, 1938
Welleraspis newfoundlandensis Lochman, 1938
Avonaspis missouriensis Lochman, 1940
Lonchocephalus swartzi Tasch, 1951
L. waddlei Tasch, 1951
Coosella vulgaris Tasch, 1951

Family CATILLICEPHALIDAE Raymond, 1938

Description.—Small (mostly 4–15 mm.), compact trilobites, micropygous to isopygous, with few (probably six to eight) thoracic segments. Glabella well defined at least laterally, subovate, parallel-sided, expanded forward, or hemispherical. Glabella furrows impressed in all but the most highly specialized forms, posterior pair invariably tending to turn backward, in many cases almost isolating subrectangular basal lobes. Occipital furrow deep even in the smoothest genera, occipital ring simple or more frequently spinose. Fixed cheeks usually convex and downsloping; ocular ridges impressed at least in the earlier genera of the family, palpebral lobes usually of medium length, located at or in advance of the glabellar midpoint, narrow in primitive genera, wider in some of the later, more specialized forms. Anterior facial sutures parallel or convergent. Frontal limb greatly reduced or entirely absent. Rostrum present in earlier forms, lacking in later genera which possess a median (asaphid) suture on the cephalic doublure. Posterior branch of facial suture opisthoparian in forms with genal spines (e.g. *Theodenisia*), reaching margin at genal angle (amphipar-

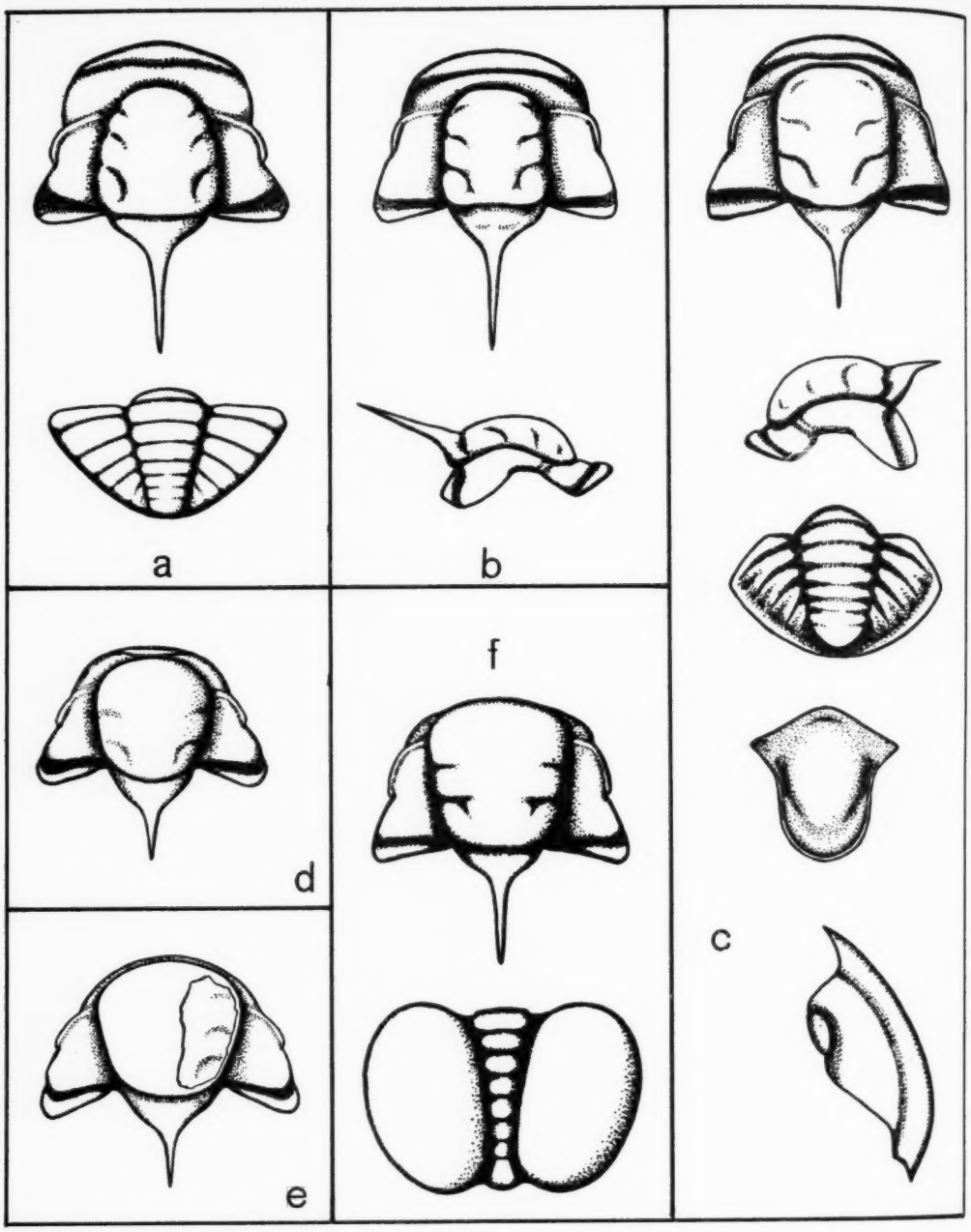

FIG. 1—*a*, *Lonchocephalus chippewaensis* Owen. Cranidium and pygidium, ×4. Dresbach sandstone, Eau Claire, Wisconsin. (p. 600)

b, *Welleraspis swartzi* (Tasch). Top and side views of cranidium, ×5. Warrier limestone, Bedford, Pennsylvania. (p. 609)

c, *Welleraspis jerseyensis* (Weller). Top and side views of cranidium, pygidium and free cheek, ×5; hypostoma, ×10. Limeport limestone, New Hope, Pennsylvania. (p. 601)

d, *Distazeris acuta* Raymond. Cranidium, ×8. Rockledge limestone, St. Albans, Vermont. (p. 603)

e, *Distazeris rasettii* Shaw, Cranidium, with right part of glabella exfoliated to show furrows on internal cast, ×8. Dresbachian boulder in conglomerate. Grosses Roches, Quebec. (p. 603)

f, *Pemphigaspis bullata* Hall. Cranidium and pygidium, ×6 (after Palmer). Dresbach sandstone, Minnesota. (p. 603)

ian) in genera lacking genal spines (*Catillicephala, Madarocephalus*).

Thorax known in few genera, with strongly marked dorsal furrows. Pygidium variable in relative size and shape, lacking marginal spines in all genera where known. Axis always well marked by dorsal furrows, of four to seven visible segments, usually prominent above pleural lobes and occupying large fraction of pygidial area (see, however, *Pemphigaspis*). Pleural furrows and interpleural grooves impressed in some of the genera. Surface of test smooth to granulate or tuberculate.

Stratigraphic and geographic range.—Upper Cambrian (Dresbachian to Trempealeauian) of North America.

Remarks.—The family Catillicephalidae as here construed includes a variety of genera, comprising aberrant forms like *Pemphigaspis*. However, at least the close relationship of the Dresbachian forms among themselves, and with the previously discussed genera *Lonchocephalus* and *Welleraspis*, is well substantiated. Less certain is the relationship between all these and the Trempealeauian genera. We know only one genus of the group from the Franconian, *Buttsia*, and this cannot yet be connected by an unbroken series of forms to the Dresbachian and Trempealeauian genera. The doubt is strengthened by the observation that the Dresbachian genera, whenever the cephalic doublure is known (*Welleraspis, Catillicephala*), show a rostrum, while the Trempealeauian *Theodenisia* has instead a median suture. Were this important feature known in all the genera, it would supply a valid character at least for subfamily distinction. Nevertheless, the glabellar features, rightly considered as more important (Henningsmoen, 1951), are so similar that close relationship of the Dresbachian and Trempealeauian genera seems probable in spite of the difference in the character of the ventral cephalic sutures. Apparently the rostrum became narrower and narrower until it was completely eliminated at a still undetermined stage in the evolution of the family.

Genus DISTAZERIS Raymond, 1937
Text-figures 1d, e

Known from the cranidium alone. Glabella similar to that of *Welleraspis*, but pyriform rather than parallel-sided; glabellar and occipital furrows, occipital ring as in *Welleraspis*. Area of frontal limb considerably reduced longitudinally, and also transversely by the convergence of the anterior branches of the facial sutures. Differentiation between brim and border faintly preserved (*D. acuta*) or entirely obsolete (*D. simplex, D. rasettii*). Marginal furrow on posterior limbs very deep, turning forward distally; this suggests rounded genal angles and amphiparian sutures as in *Catillicephala*. Fixed cheeks, ocular ridges and palpebral lobes as in *Welleraspis*.

Type species.—*Distazeris acuta* Raymond, 1937.

Stratigraphic and geographic range.—Dresbachian of the Appalachian province.

Remarks.—*Distazeris* evidently is a *Welleraspis* modified chiefly by reduction of the frontal limb; *D. acuta* and *D. rasettii* (figs. 1d, 1e) represent two progressive stages in this reduction. Further obliteration of the frontal limb produced *Catillicephala*.

Species assigned to the genus.—
Distazeris acuta Raymond, 1937
Ucebia simplex Raymond, 1937
Distazeris rasettii Shaw, 1952

Genus PEMPHIGASPIS Hall, 1863
Text-figure 1f

Description.—Cephalon strongly convex. Glabella straight-sided, expanded forward, with deep glabellar furrows, the posterior ones often bifurcating at the inner end and with one branch directed backward. Occipital ring with spine. Fixed cheeks convex, ocular ridges, palpebral lobes and posterior limbs as in *Welleraspis*. Frontal limb entirely or almost obsolete, at most represented by a narrow undifferentiated band not visible from above as it is covered by the tumid front of the glabella. Free cheeks narrow, with wide convex border and long genal spines. Eyes long and narrow. Thorax of eight plus segments; axis prominent, dorsal furrows deep. Pygidium with axis much narrower than thoracic axis, tapered posteriorly, usually deeply sunk between tumid pleural lobes, reaching the posterior margin. Axis with numerous furrows. Pleural lobes tumid, oval, unfurrowed, rimless, with convexity continuing onto the doublure anteriorly, laterally and posteriorly.

Type species.—*Pemphigaspis bullata* Hall, 1863.

Synonym.—*Hallaspis* Raasch and Lochman, 1943 (type: *Amphion? matutina* Hall, 1863 = *Pemphigaspis bullata* Hall).

Stratigraphic and geographic range.—Dresbachian of the Appalachian, Central and Cordilleran provinces of North America.

Remarks.—The cephalon of this genus is so similar to those of *Welleraspis* and *Distazeris* that close relationship seems unquestionable notwithstanding the aberrant pygidium. This part of the exoskeleton was long considered a cranidium or a problematic fossil, and the two shields received by Hall separate names that were perpetuated in the literature. Palmer (1951) showed that they belong to the same trilobite, and gave an excellent redescription of the genus on this basis. The type species is illustrated in figure 1f.

Species assigned to the genus.—

Pemphigaspis bullata Hall, 1863 (= *Amphion? matutina* Hall, 1863; *?Pemphigaspis appalachia* Resser, 1938).

Pemphigaspis inexpectans Lochman, 1938.

P. intermedia Tasch, 1951 (= *?P. bullata waddlensis* Tasch, 1951).

Genus CATILLICEPHALA Raymond, 1938
Test-figure 2b

Description.—Cephalon strongly convex. Glabella hemispherical or expanded forward, highly convex, defined laterally by deep dorsal furrows, overhanging the front of the cephalon; glabellar furrows usually obsolete at least on external surface; when present (*C. fowleri*), posterior pair showing course characteristic of the family. Occipital furrow deep, occipital ring rounded. Frontal limb obsolete, or possibly present as a narrow (sag.) band undifferentiated from the glabella. Fixed cheeks downsloping. Ocular ridges indistinct; palpebral lobes small, opposite glabellar midpoint and close to glabella. Visual surface of eye highly convex. Posterior branch of facial suture reaching margin at rounded genal angle. Anterior branch directed forward and inward, marginal portion somewhat arched at midline. Doublures of free cheeks separated by hourglass-shaped rostrum.

Thorax with strongly convex axis; pleura not extended into spines. Pygidium subtriangular, with long, strongly prominent axis almost reaching posterior margin. Pleural lobes slightly downsloping, with faint marginal furrow and indistinct segmentation. Margin downrolled into narrow doublure. Surface of test smooth.

Type species.—*Cephalocoelia ovoides* Raymond, 1937.

Synonym.—*Cephalocoelia* Raymond, 1937 (non *Cephalocoelia* Etallon, 1859).

Stratigraphic and geographic range.—Dresbachian of the northern Appalachians.

Remarks.—Recent discussions of the genus by Rasetti (1946), Wilson (1951) and Shaw (1952) make further remarks unnecessary. Shaw identified *Cephalocoelia ovoides* Raymond, the type species of *Cephalocoelia* (subsequently replaced with *Catillicephala*) with *Ucebia lata* Raymond and therefore changed the name of the type species to *Catillicephala lata*. This synonymy is possibly correct, but the poor state of preservation of the type material does not allow any degree of certainty, hence the writer prefers to preserve the original designation of the type species. Shaw also placed *Catillicephala rotunda* (Rasetti) in synonymy with *C. lata*, a procedure with which the writer is inclined to disagree. The two forms are very similar, yet the differential characters are constantly observed in the several scores of specimens known for each species. It is possible, however, that *C. rotunda* is synonymous with *C. ovoides*.

Fig. 2b illustrates *Catillicephala impressa* Rasetti.

Species assigned to the genus.—

Cephalocoelia ovoides Raymond, 1937

Ucebia lata Raymond, 1937

Cephalocoelia impressa Rasetti, 1946

C. rotunda Rasetti, 1946

Catillicephala fowleri Shaw, 1952

Genus MADAROCEPHALUS Resser, 1938
Text-figure 2a

Description.—Cephalon alone known. Cephalon highly convex; glabella well defined, straight-sided, expanded forward, overhanging the anterior cephalic margin. Glabellar furrows indistinct, occipital furrow impressed, occipital ring bearing a spine. Palpebral lobes small, situated in very anterior position and close to glabella. Frontal

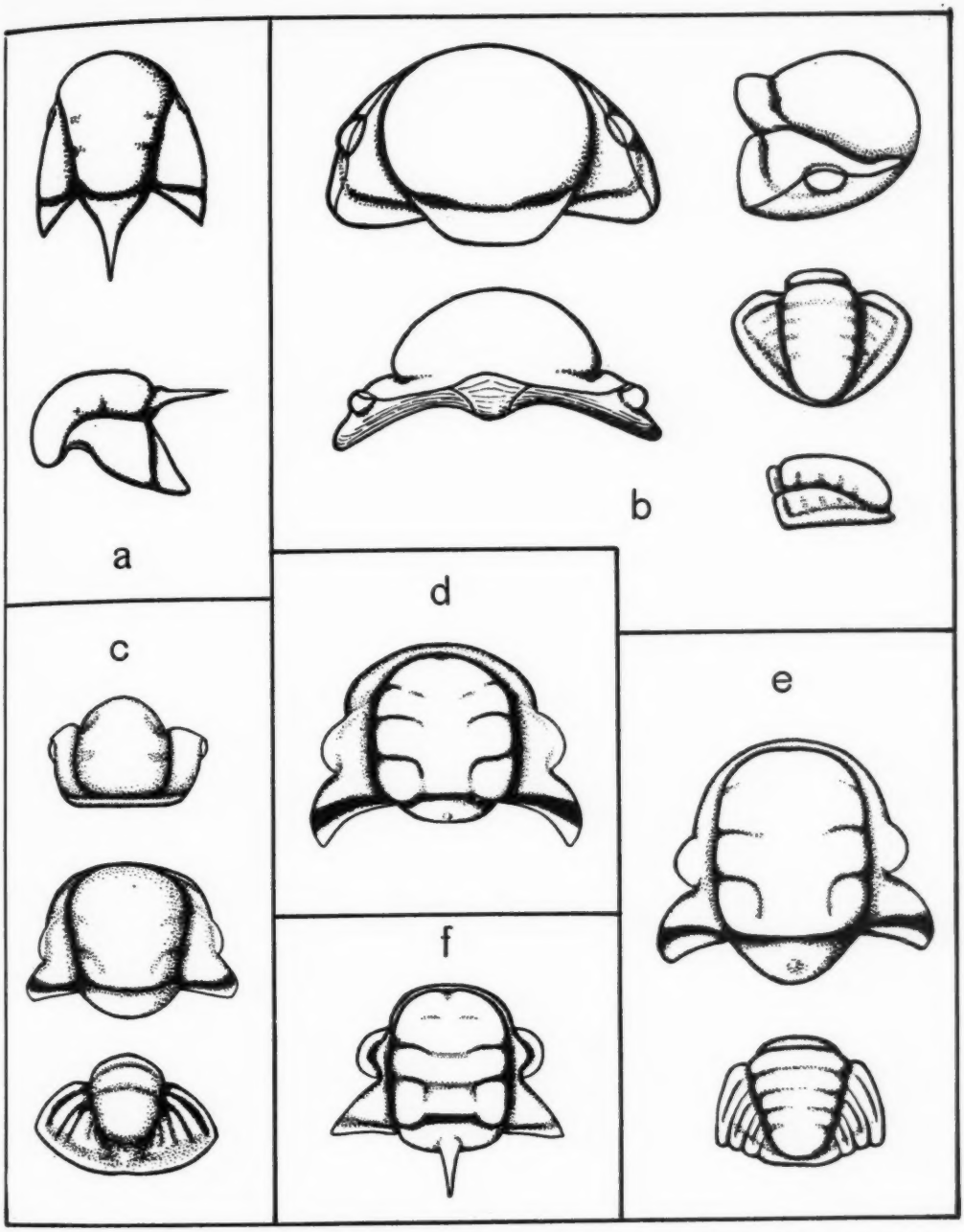

FIG. 2—*a*, *Madarocephalus minor* Rasetti. Top and side views of cranidium, ×12. Dresbachian boulder in conglomerate, Metis, Quebec. (p. 604)

b, *Catillicephala impressa* (Rasetti). Top, front, and side views of cephalon; top and side views of pygidium, ×6. Dresbachian boulder in conglomerate, Grosses Roches, Quebec. (p. 604)

c, *Buttsia drabensis* Wilson. Front and top views of cranidium, ×3; pygidium, ×4 (after Wilson). Ore Hill limestone, Drab, Pennsylvania. (p. 606)

d, *Triarthropsis nitida* Ulrich in Bridge. Cranidium, ×5. Eminence dolomite, Potosi, Missouri. (p. 606)

e, *Triarthropsis marginata* (Rasetti), Cranidium and pygidium, ×10. Trempealeauian boulder in conglomerate, Levis, Quebec. (p. 606)

f, *Stenochilina spinifera* Ulrich in Bridge. Cranidium, ×4. Eminence dolomite, Potosi, Missouri. (p. 606)

limb obsolete. Posterior branch of facial suture reaching margin at genal angle; anterior branch reaching margin at short distance from eye, thence marginal. Marginal furrow deep on posterior limbs, indistinct on free cheeks.

Type species.—*Madarocephalus laetus* Resser, 1938.

Stratigraphic and geographic range.—Dresbachian of the Appalachian province.

Remarks.—The genus seems closely allied to *Catillicephala*, from which it differs in the straight-sided glabella, anterior position of eyes, and occipital spine.

Species assigned to the genus.—Besides the type species, the genus includes *M. minor* Rasetti, 1946. This species is illustrated in figure 2a.

Genus BUTTSIA Wilson, 1951
Text-figure 2c

Description.—Cephalon highly convex. Glabella tumid, expanded forward, almost reaching anterior margin of cranidium. Glabellar furrows faint, occipital furrow well impressed, occipital ring rounded. Brim obsolete, border a narrow (sag.), convex band. Fixed cheeks convex, slightly downsloping; palpebral lobes small, at level of glabellar midpoint, distant from glabella about one-fourth of glabellar width. Posterior limbs deeply furrowed. Anterior facial sutures parallel in front of eyes; posterior branch reaching margin inside genal angle. Pygidium with prominent axis occupying about two-thirds of length; axis of few segments. Pleural lobes downsloping, with a few furrows and grooves impressed. Border poorly defined.

Type species.—*Buttsia drabensis* Wilson.

Stratigraphic and geographic range.—Early Franconian of the central Appalachians.

Remarks.—Wilson compared *Buttsia* with *Catillicephala*, "*Hallaspis*" and "*Acheilus*?" and the writer agrees in considering it a relative of these genera, although no intermediate forms are known. In the cranidial features, *Buttsia* is rather similar to *Catillicephala*, differing in the presence of a distinct border and in the course of the posterior branch of the facial suture. The pygidium, however, is considerably different from that of *Catillicephala* and somewhat intermediate between those of *Welleraspis* and the Trempealeauian genera *Triarthropsis* and *Theodenisia*.

The type species (Fig. 2c) is the only one assigned to the genus.

Genus STENOCHILINA Ulrich in Bridge, 1930
Text-figure 2f

Description.—Glabella parallel-sided, rounded in front, well defined by the dorsal furrow. Glabellar furrows impressed, faintly joined across the glabella; posterior pair bifurcated, with posterior branch curving backward and almost isolating basal lobes. Occipital furrow deep, occipital ring spinose. Frontal limb reduced to a narrow (sag.), wire-like, undifferentiated band. Palpebral lobes very close to glabella, of medium size, bowed, set off by a distinct palpebral furrow, situated well in front of glabellar midpoint. Anterior branch of facial suture closely following glabellar outline; posterior branch almost straight, producing triangular posterior limbs.

Type species.—*Stenochilina spinifera* Ulrich in Bridge, 1930.

Stratigraphic and geographic range.—Late Trempealeauian of the Ozark region, Missouri.

Remarks.—The genus is placed in the family because it seems difficult to doubt its close relationship to *Triarthropsis*, evidenced by many common features of the cranidia. The type species (Fig. 2f) is the only one assigned to the genus. Other forms described as *Stenochilina* are either unidentifiable or belong in other genera.

Genus TRIARTHROPSIS Ulrich in Bridge, 1930
Text-figure 2 d–e

Description.—Glabella moderately convex, parallel-sided, well rounded in front, well defined by the dorsal furrow. Glabellar furrows impressed, posterior pair turning backward and almost isolating basal lobes. Occipital furrow well marked, occipital ring rounded. Anterior limb reduced to a narrow (sag.), convex, undifferentiated band. Palpebral lobes of medium size, opposite glabellar midpoint and close to glabella; palpebral furrow shallow or obsolete. Posterior limbs deeply furrowed, somewhat falcate (*T. nitida*). Anterior facial suture directed forward in front of eye, gradually curving inward and rounding off anterior margin of cranidium. Posterior branch

gradually curving backward and slightly inward before reaching margin. Free cheeks with short genal spines (*T. marginata*). Pygidium (*T. marginata*) with prominent axis almost reaching posterior end, of four segments plus terminal section. Pleural lobes steeply downsloping, with furrows and grooves.

Type species.—*Triarthropsis nitida* Ulrich in Bridge, 1930.

Stratigraphic and geographic range.—Late Trempealeauian of Appalachians and Ozark region.

Remarks.—The genus seems closely related to *Theodenisia*, from which it differs essentially in the development of the frontal limb. The type and another species are illustrated in figures 2d, 2e.

Species assigned to the genus.—

Triarthropsis nitida Ulrich in Bridge, 1930

Ptychoparia blairi Weller, 1903

Acheilus? marginatus Rasetti, 1945

Genus THEODENISIA Clark, 1948
Text-figure 3 a–e

Description.—Glabella of variable convexity, well defined by the dorsal furrow at least laterally, anteriorly reaching the margin of the cranidium or merging without change of slope into a narrow (sag.), undifferentiated frontal limb. Glabella usually straight-sided, expanded forward, sometimes parallel-sided, rarely ovate (*T. eminens*). Glabellar furrows deeply to faintly impressed (one to four pairs visible), posterior pair invariably turning backward and almost isolating subquadrate basal lobes. Occipital furrow deep, occipital ring usually rounded, rarely (*T. spinosa*) spinose. Fixed cheeks horizontal or downsloping; palpebral lobes usually of medium size, close to glabella and at level of glabellar midpoint; rarely (*T. microps*) small and more anteriorly situated. Palpebral furrow weak to almost obsolete. Posterior limbs of variable shape, from slender and long (tr.) in *T. marcoui* to shorter (tr.) and wider (exsag.) in *T. lata* and *T. eminens*, rarely broadly triangular (*T. microps*). Marginal furrow on posterior limbs very deep. Anterior facial sutures directed somewhat inward in front of eyes, soon reaching anterior margin near obsolete end of dorsal furrow; marginal portion straight. Posterior branch usually curving slightly inward before reaching margin. Doublures of free cheeks separated by median suture (*T. lata, T. spinosa*). Free cheeks with genal spines, with possible exceptions (*T. microps*). Visual surface of eye crescentiform, visibly faceted.

Thorax partially known, of six plus segments (*T. lata*). Axis very prominent; pleural geniculation very close to dorsal furrow; pleural terminations rounded. Pygidium small, occupying almost vertical position when thorax is horizontal. Axis large, prominent, of few segments, rarely (*T. marcoui*)with a dorsal spine. Pleural lobes steeply downsloping, showing furrows and grooves; border indistinct, margin smooth.

Type species.—*Denisia eminens* Clark, 1924.

Stratigraphic and geographic range.—Late Trempealeauian of Appalachians, the Ozark region, and the Cordilleran province.

Synonyms.—*Denisia* Clark, 1924 (non Hübner, 1825); *Acheilus* Raymond, July 1924 (non Clark, June 1924).

Remarks.—The genus as here construed includes a rather large number of species, variable in most of the cranidial features to a greater extent than usually allowed among Cambrian trilobites. However, it would be difficult to separate clear-cut genera, because those species which are similar in some respects differ in others. Since it is possible to bridge the gaps, through described or undescribed species, between any forms here assigned to the genus, the writer considers the close relationship among them as unquestionably proven. The illustrations (Fig. 3) show five different species, representing the most characteristic groups within the genus.

A nomenclatural note is necessary to explain the present use of the name *Theodenisia* for the species which have been usually placed, by the writer and others, in *Acheilus*. The nomenclautral history of *Acheilus* was recently reviewed by Shaw (1952). The genus was usually credited to Raymond (July 1924) who described it, naming as type species *Acheilus marcoui*. However, Clark (June 1924) had inadvertently published *Acheilus* as a monotypic genus by describing a species, *Acheilus levisensis*. Hence the rules of nomenclature require that, if *Acheilus* is used at all, it be credited to Clark and the type species be *A.*

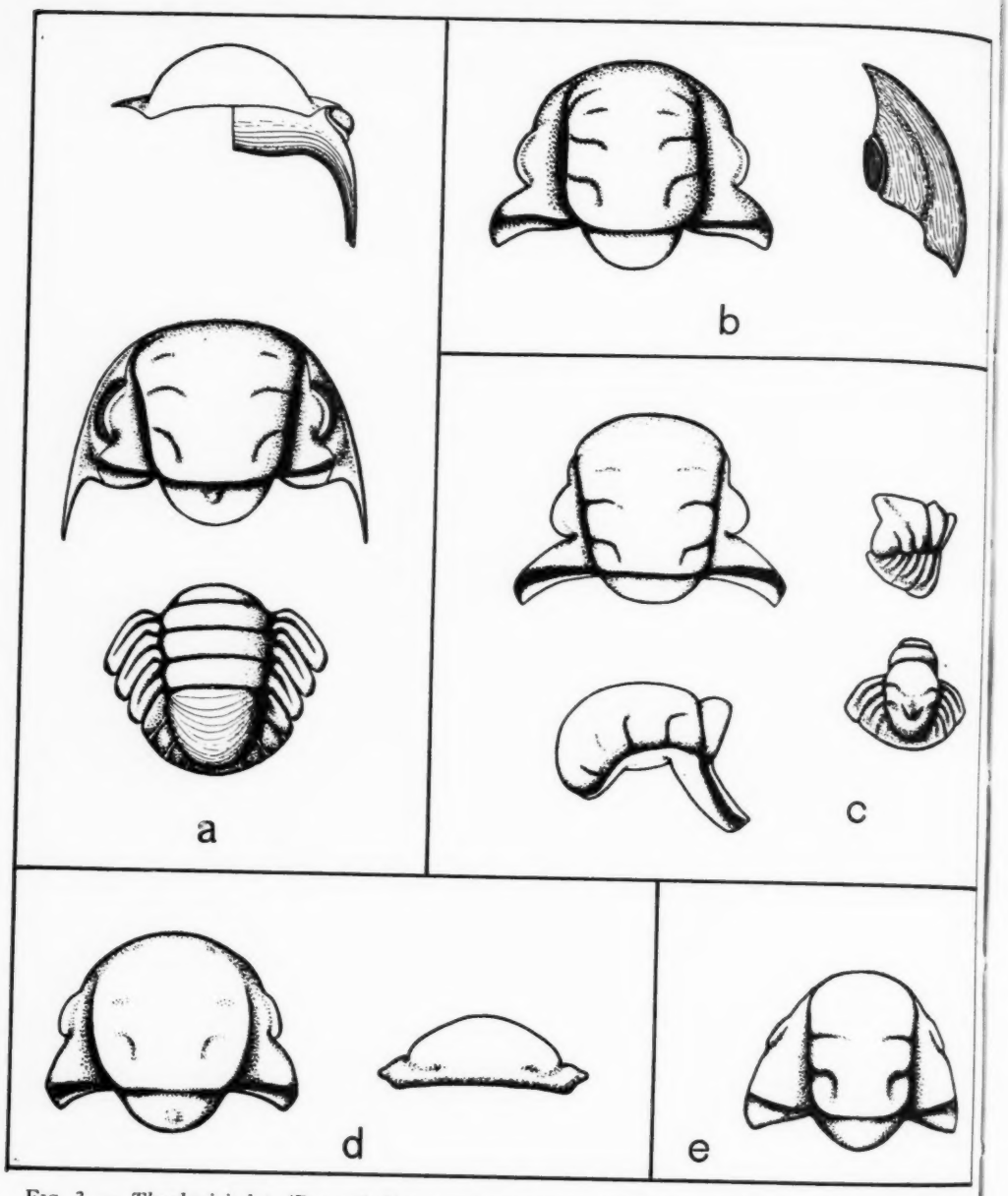

FIG. 3—*a*, *Theodenisia lata* (Rasetti). Front and top views of cephalon; pygidium with 3 thoracic segments attached, ×10. Trempealeauian boulder in conglomerate, Levis, Quebec. (p. 607)
b, *Theodenisia communis* (Rasetti). Cranidium and free cheek, ×10. Trempealeauian boulder in conglomerate, Levis, Quebec. (p. 607)
c, *Theodenisia marcoui* (Raymond). Top and side views of cranidium; side and top views of pygidium, ×6. Trempeauleauian boulder in conglomerate, Levis, Quebec. (p. 607)
d, *Theodenisia eminens* (Clark). Top and front views of cranidium, ×10. Trempleauleuian boulder in conglomerate, Levis, Quebec. (p. 607)
e, *Theodenisia microps* (Rasetti). Cranidium, ×15. Trempealeauian boulder in conglomerate, Levis, Quebec. (p. 607)

levisensis. Unfortunately, the holotype and only known specimen of *A. levisensis* is an immature and imperfectly preserved cranidium which the writer considers generically and specifically unidentifiable. In the present case, it would be of no avail to look for better-preserved topotype material, since the specimen was collected from a pebble. The only satisfactory solution which does not require use of the plenary powers of the International Commission on Zoological Nomenclature (an intervention which does not seem warranted by the importance of the case) is to disregard *Acheilus levisensis* and hence the generic name *Acheilus* (although *Acheilus* Clark, June 1924 is nomenclaturally valid). Fortunately, the species hitherto placed in *Acheilus* can be assigned to another genus erected by Clark, *Denisia*, which was subsequently found preoccupied and replaced by *Theodenisia*.

Species assigned to the genus.—
Denisia eminens Clark, 1924 (=*Denisia pusilla* Clark, 1924)
Ptychoparia newtonensis Weller, 1903
Acheilus macrops Raymond, 1924
A. marcoui Raymond, 1924
Triarthropsis princetonensis Kobayashi, 1935
Acheilus brevis Rasetti, 1944
A. communis Rasetti, 1944
A. depressus Rasetti, 1944
A. gibbus Rasetti, 1944
A. latus Rasetti, 1944
A. limbatus Rasetti, 1944
A. microps Rasetti, 1944
A. convexus Rasetti, 1945
A. spinosus Rasetti, 1945
A. triangularis Rasetti, 1945

ONTOGENY OF *Welleraspis*

WELLERASPIS SWARTZI (Tasch)

Plate 62, figure 1–15; text-figures 1b, 4a–c

Lonchocephalus swartzi TASCH, 1951, Jour. Paleontology, vol. 25, p. 300, pl. 45, figs. 16, 17.

Certain beds of the Warrior limestone collected at the type locality for *Welleraspis swartzi* (Tasch) showed hundreds of fragments of this species, to the almost complete exclusion of other trilobites. Careful examination revealed well-preserved larval forms, ranging from metaprotaspis to later stages. Both the above-mentioned character of the deposit, and the unbroken sequence of growth stages observed, insure that we are dealing with individuals belonging to one species. Since very few ontogenies of North American Cambrian trilobites have been published (owing not to scarcity of larval forms but to difficulty in assigning them to definite adult species), the material seems worthy of a brief description.

The earliest stage observed is represented by two metaprotaspis specimens, complete except for lack of the free cheeks (Pl. 62, figs. 1–4; text-figs. 4a, b.). One is 0.40 the other 0.45 mm. long in dorsal view. The shield is highly convex in both directions, the frontal portion of the glabella turning down steeply, while the pygidial part is almost vertical with respect to the average plane of the cephalic surface. The fixed cheeks also slope down steeply at the sides. The glabella is well defined by a deep dorsal furrow and shows four lobes, plus the occipital ring, all separated by well-impressed furrows. The occipital furrow and the third glabellar furrow are impressed all the way across the axis; the glabellar furrows of the second pair are connected across the glabella by a shallower portion; those of the first pair are well impressed only at the sides. The lobes thus defined appear of approximately equal length in dorsal view,

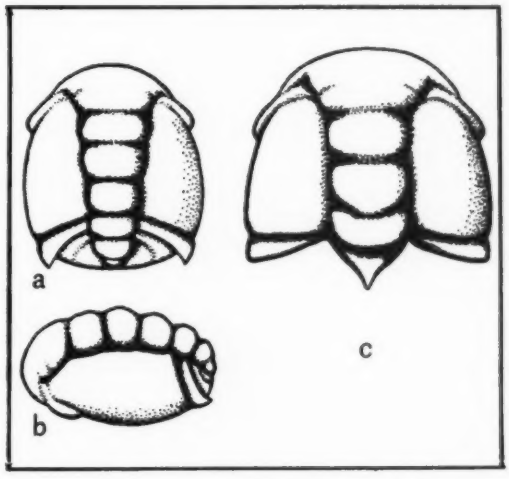

FIG. 4—*Welleraspis swartzi* (Tasch). *a, b*, Top and side views of metaprotaspis lacking the free cheeks, ×60. *c*, Meraspis cranidium, ×60. See also figure 1b and plate 62.

except that the occipital ring is somewhat shorter than the others. Actually the frontal lobe is considerably longer, appearing shortened on account of its convexity. The frontal lobe shows indication of further segmentation by a pair of exceedingly short and shallow furrrows at the sides, a feature barely observable on the whitened specimens under appropriate lighting. The glabella expands forward, slightly from the occipital furrow to the first glabellar furrow, then rapidly in the frontal lobe; it reaches the margin of the cephalon. The sides of the frontal lobe are continuous with a pair of low, short ridges which form the cephalic border for some distance. This marginal ridge is separated by a narrow, shallow depression from the ocular ridges and palpebral lobes, not clearly differentiated from each other. The average position of the rather short palpebral lobes is opposite the anteriormost glabellar furrow. Behind the palpebral lobes, the margin of the fixed cheeks (i.e., the posterior branch of the facial suture) proceeds backward with slight curvature. The occipital furrow is extended onto the fixed cheeks by a well-impressed furrow, which becomes the posterior marginal furrow of the cephalon in later stages, and is followed by a prominent border. This border is apparently extended at the posterolateral angles into a pair of short spines. Behind the border, the pygidial portion of the metaprotaspis dips down steeply and rapidly tapers in width. The axis remains prominent and reaches the posterior end of the shield, showing a distinct ring plus a terminal section. The pleural lobes indicate a pair of furrows. The pygidial area is so small that its features are somewhat difficult to ascertain.

The next stages observed are represented by meraspis cranidia ranging from 0.5 mm. up in length. The smaller meraspis cranidia (Pl. 62, figs. 5, 6) are not substantially different from the corresponding part of the above-described metaprotaspis. The chief modifications in the axial part of the shield occur in the glabellar and occipital furrow. While the latter remains deeply impressed throughout, the glabellar furrows gradually assume the character of pairs of lateral furrows; at this stage, a faint connection across the glabella still subsists. The occipital ring begins to develop a short occcipital spine. The frontal lobe of the glabella is still extended into anterior marginal ridges, hence the dorsal furrows do not reach the margin of the cephalon.

When the meraspis cranidium attains a length of 0.6–0.7 mm. (Pl. 62, fig. 7), an exceedingly narrow (sag.) border begins to appear in front of the glabella, continuous with the above-mentioned marginal ridges at the sides, both together forming the anterior cephalic border. The glabella does not expand forward as much as in earlier stages. The glabellar furrows become essentially confined to the sides, and only those of the posterior pair maintain considerable depth. The occipital spine increases in relative length. The palpebral lobes slowly migrate backward.

A meraspis cranidium 0.84 mm. long (Pl. 62, fig. 8) shows a much better defined anterior border, glabella almost parallel-sided, and well-developed occipital spine.

After this stage, the anterior border begins to assume the convex wire-like shape of the adult, and a narrow (sag.) brim makes its appearance. The glabella becomes proportionately shorter and wider and no longer expands forward, A cranidium of this type 1.1 mm. long (excluding the occipital spine) is shown on Plate 62, figure 9. The cephalon at this stage begins to resemble closely that of the adult. It is possible that from here on we are dealing with holaspis stages, although there is no evidence on this point, since no specimens preserving thorax and pygidium could be found.

The next crandium illustrated (Pl. 62, fig. 10) is 1.9 mm. long. It differs from the preceding chiefly in the still more posterior position of the palepbral lobes, and has essentially the same shape as a cranidium 5 mm. long (Pl. 62, figs. 11, 13) which is about two-thirds of the largest observed.

The protaspis here described closely resembles that of *Olenus gibbosus* (Størmer, 1942) in many details, such as the distinctness of the dorsal furrows, shape of the glabella, structure of the anterior border and ocular ridges. The advanced meraspis stages are remarkable for the resemblance of the cranidia to those of small corynexochid trilobites. At this stage the ptychopariid affinities of the species, obvious in the adult,

are not apparent. Similar features were observed by Barrande (1852) in the ontogeny of *Sao hirsuta*.

PHYLOGENY

Relationships among the genera discussed in this paper have been already pointed out and may be summarized as follows. The series *Lonchocephalus—Welleraspis—Distazeris—Catillicephala* indicates that the latter genus, hence presumably other Upper Cambrian trilobites with expanding glabella (*Madarocephalus*, *Buttsia*, *Theodenisia*) do not descend from the Corynexochidae, as it had been previously assumed, but are specialized offshoots of the ptychopariid stock. Although the writer believes that the above-mentioned series represents the approximate morphologic changes that have occurred in a phylogenetic line, it cannot be assumed that the four genera are descendants of each other, because they are not successive in time. They are almost contemporary, and *Catillicephala*, although believed to represent the last evolutionary step is actually known from somewhat older strata than *Lonchocephalus* and *Welleraspis*. This fact does not contradict the assumed interpretation and frequently occurs in paleontology. A genus *A* giving rise to a more specialized genus *B*, may well continue to exist simultaneously with its descendant, and even outlive it. Hence, owing to incompleteness of the fosssil record, we may only know *A* from strata younger than those containing *B*. In the present instance, the writer believes that *Catillicephala* did not arise from *Lonchocephalus*, but from genera similar to *Lonchocephalus* living in the late Medial Cambrian. Search for such direct ancestors reveals a number of candidates, e.g., *Ehmania*, *Armonia*, *Metisia*, etc. Until the latest Medial Cambrian faunas become better known, we cannot hope to ascertain a detailed line of descent, but the writer beileves that the ancestors of *Lonchocephalus* and *Welleraspis*, and hence of the Catillicephalidae, cannot be far from the above-mentioned genera.

It also appears that the ancestral ptychopariid stock of *Lonchocephalus* and *Welleraspis*, having produced the specialized Cattillicephalidae, continued to give rise to less specialized, still solenopleuriform genera through the entire Late Cambrian epoch. Among such possible relatives, in the Dresbachian one might mention "*Albansia*" (as represented by *Albansia? montanesnis*), *Amiaspis*, *Geneivevella*, *Raaschella*, *Tablotina*, *Terranovella*, and *Weeksina*, all characterized by the same type of glabellar furrows. In the Franconian, *Berkeia*, *Kindbladia* and *Sulcocephalus*; in the Trempealeauian, *Calymenidius* and *Glyptometopus*.

The genus *Acheilops* deserves special discussion. Ulrich considered it a close relative of "*Acheilus*," then assigned to the Corynexochidae. Now that "*Acheilus*" (*Theodenisia*) is shown to have no relationship with that family, the systematic position of *Acheilops* becomes questionable. The cranidium, the only known part, remarkably resembles such Medial Cambrian corynexochids as *Glossopleura*. However, the example of *Theodenisia* has taught us to mistrust such resemblances as indicative of affinity. Possibly the question will be decided when the ventral cephalic sutures of *Acheilops* become known. If it is a corynexochid, it will probably show a rostrum fused with the hypostoma (Rasetti, 1952); if it is a ptychopariid, it will either have a separate rostrum like *Catillicephala* or a median (asaphid) suture like *Theodenisia*.

These considerations indicate that superficial appearance can be misleading in assessing the relationships of Cambrian trilobites. Especially such features as extent, structure, and even presence or absence of frontal limb, are susceptible of rapid change, hence can be used for generic, possibly sometimes for family distinction, but certainly have no deeper significance. The present study confirms the point emphasized by Henningsmoen (1951) that characters of the axial portions of the exoskeleton are much more likely to be significant, corresponding to important organs of the animal. In agreement with this principle, the genera here discussed were united chiefly on the basis of the common shape of the glabellar furrows. The ventral cephalic sutures may supply other important taxonomic characters (Rasetti, 1952); unfortunately, they are at present known in too few forms to be of much use.

A further consideration suggested by the

"corynexochid" appearance of *Theodenisia*, *Madarocephalus*, and to a lesser extent of other genera here assigned to the Catillicephalidae, is their resemblance to the meraspid carnidia of such ptychopariids as *Welleraspis*. One should compare, for example, the adult cranidium of *Theodenisia microps* (Fig. 3e) with the meraspid cranidium of *Welleraspis swartzi* (Fig. 4c). This similarity, coupled with the fact that adult individuals of *Theodenisia*, *Madarocephalus*, etc., are very small, suggests that the latter genera retained in the adult such juvenile features as the "corynexochid" shape of the glabella and the small size. Similar examples of "neoteny" are known in many groups of living and fossil organisms.

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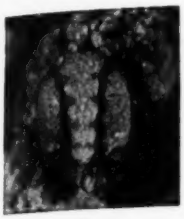
MANUSCRIPT RECEIVED SEPTEMBER 22, 1953

EXPLANATION OF PLATE 62

FIGS. *1–15*—*Welleraspis swartzi* (Tasch). Warrior limestone, about 100 feet below top of formation; road cut on N side of Pennsylvania Turnpike, 2.5 miles east of Bedford, Pennsylvania (Wilson's locality 47–11w.1). *1*, metaprotaspis, ×40. *2*, *3*, two top views of a slightly larger metaprotaspis, ×40, with somewhat different lighting. *4*, side view of the same specimen, ×40. *5*, meraspis cranidium, ×40. *6*, another meraspis cranidium, ×40. *7*, larger meraspis cranidium, ×40. *8*, meraspis cranidium showing distinct border, ×30. *9*, small holaspis (?) cranidium, ×20. *10*, larger holaspis cranidium, ×10. *11*, *12*, side and top views of almost full grown cranidium, ×6. *13*, doublure of free cheek showing curved anterior margin, indicating presence of a rostrum, ×10. *14*, hopostoma, ×10. *15*, pygidium, ×10. USNM 123430, plesiotypes. (p. 609)



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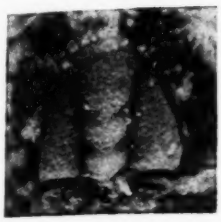

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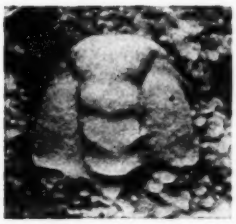

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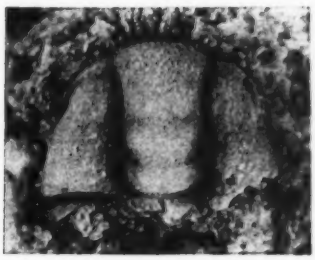

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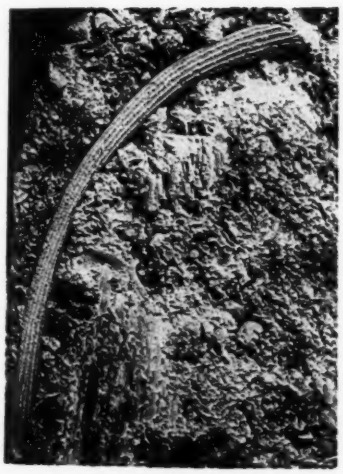

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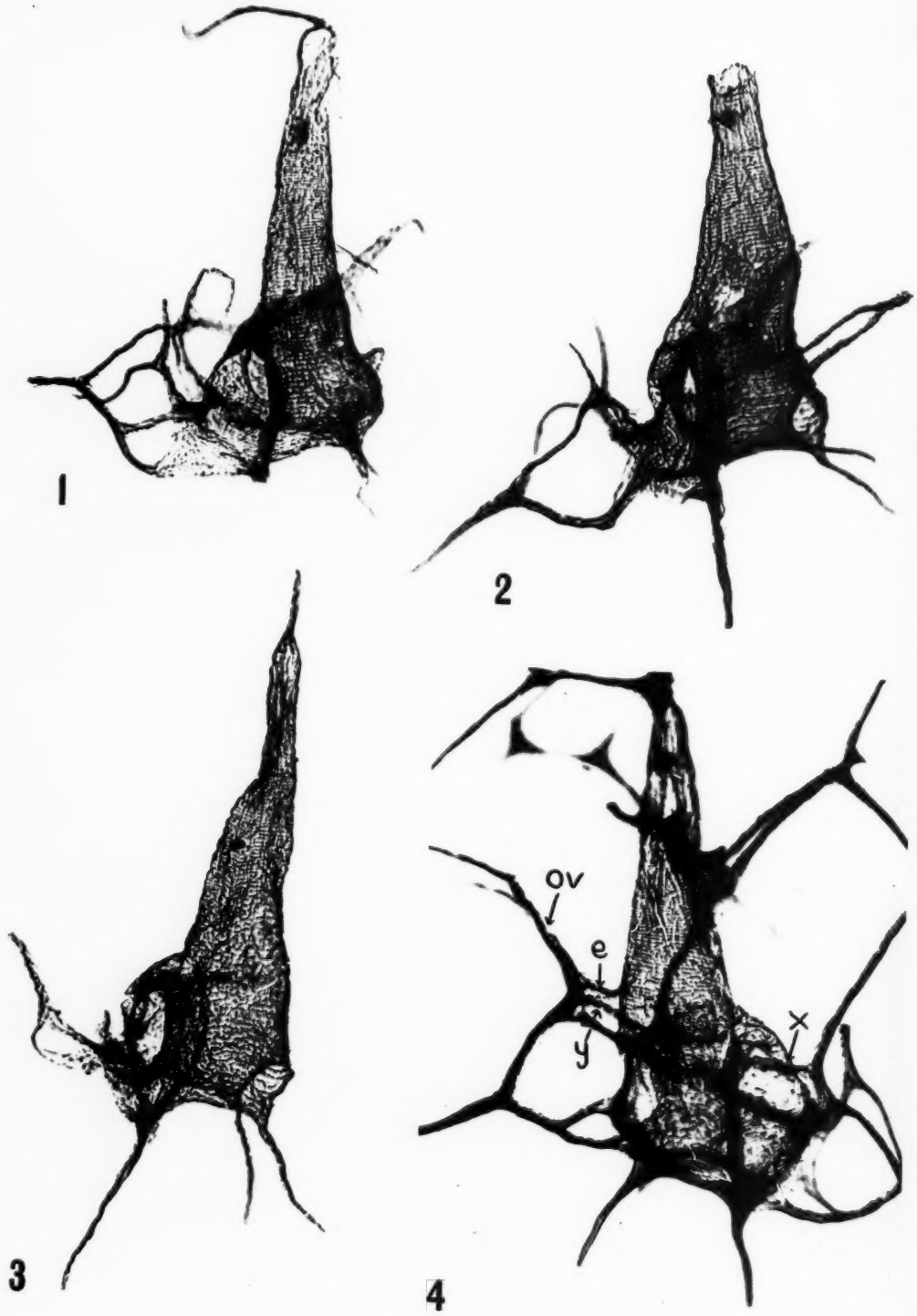
Rasetti, Catillicephalidae and *Welleraspis*



Whittington, Oklahoma Ordovician graptolite

JOURNAL OF PALEONTOLOGY, VOL. 28, NO. 5, PP. 613–621, PL. 63, 13 TEXT FIGS., SEPTEMBER 1954

A NEW ORDOVICIAN GRAPTOLITE FROM OKLAHOMA

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ABSTRACT—Isolated graptolite specimens, obtained by dissolving lower Viola limestone (Middle Ordovician) in acid, represent a new genus and species, *Orthoretiolites hami*. Sicula, initial bud, and proximal part of first three thecae with continuous periderm, remainder of rhabdosome represented by clathria only. Thecae alternating, of orthograptid type, with straight ventral wall. Development of nonseptate diplograptid type. The new genus and species is distinct from Ordovician Retiolitidae and, despite reduction of the periderm, is placed in the Diplograptidae.

INTRODUCTION

THE NEW graptolite described below was obtained by dissolving pieces of the lower Viola limestone successively in hydrochloric and hydrofluoric acid. The graptolites were picked from the resulting residue after washing, and mounted in glass slides with a small concavity. The mounting medium was that supplied by the Technicon Chemical Company, Inc., of New York City. The transfer of the delicate rhabdosomes from the residue to the mounting medium was accomplished in stages, using the dehydrant and fixative supplied by the same Company. The mounted specimens were photographed on infra-red film, which gave better results than panchromatic film. These techniques are essentially those of other workers (e.g. Bulman, 1944, pp. 1–2; Eisenack, 1935, p. 73). Because of the delicacy and fragility of the specimens described, I made no attempt to render the periderm more translucent by the use of concentrated nitric acid and potassium chlorate.

Dr. W. E. Ham kindly spent several days with me in the Arbuckle Mountains, and guided me to the locality which yielded the graptolites, I am indebted to Dr. O. M. B. Bulman for helpful advice and his critical reading of the manuscript, and to Miss Pat Washer for drawing text-figures 1–7.

TERMINOLOGY

The net-like framework or *clathria* is composed of rounded, cord-like *lists*. The lattices of lists forming the reverse and obverse sides of the rhabdosome are shown in text-figures 1, 2, and the lists are named in accordance with the terminology given by Elles and Wood (1908, pp. 304–306). An additional term, *ventral* list, is used for the lists defining the outer or ventral wall of the theca. The relation of the lattices to the early-formed continuous periderm is also indicated. The two lattices are united by crossbars—*apertural* lists outlining the lip of the external opening of the theca, and *postapertural* lists (position indicated by circles in text-figures 1, 2). The latter is an additional term, these lists running between the junctions of the pleural, ventral and parietal lists, and not between the junctions of the dorsal and parietal lists, as do the aboral lists of Elles and Wood. The term "chitin" is used for convenience, and does not imply exact knowledge of the substance forming the graptolite rhabdosome.

SYSTEMATIC PALEONTOLOGY

GRAPTOLOIDEA Lapworth, 1875
Family DIPLOGRAPTIDAE Lapworth, 1873
Genus ORTHORETIOLITES Whittington, n. gen.

Type species.—*Orthoretiolites hami* Whit-

EXPLANATION OF PLATE 63

FIGS. *1–4*—*Orthoretiolites hami* Whittington, n. gen., n. sp. Viola limestone, 100 feet above base, road cut on U. S. Highway 77, 2½ miles north of Springer, Oklahoma. *1*, obverse view, sicula and th 1^1 complete, th 1^2 and th 2^1 in early developmental stage. Compare text-figure 8. MCZ 512d. *2*, obverse view, sicula and th 1^1 complete, th 1^2 and th 2^1 in early developmental stage. Compare text-figure 9. MCZ 512e. *3*, obverse view, sicula complete, early developmental stages of th 1^1 and th 1^2. Compare text-figure 5. MCZ 512b. *4*, reverse view, rhabdosome with 3rd, 4th and 5th thecae damaged, and showing additional lists (x and y) in proximal portion. ov = obverse ventral list of th 2^2; e = parietal list of th 1^2. MCZ 512k. ×80.

(p. 614)

tington, n. gen., n. sp.

Diagnosis.—Sicula, initial bud and proximal part of th 1^1, th 2^1 and th 1^2 with continuous periderm, remainder of rhabdosome represented by clathria only, rectangular in cross section. Virgula forms central longitudinal strand of lattice on obverse side. Thecae of orthograptid type with straight ventral wall, alternating, overlapping about one-fifth of their length. Development of non-septate diplograptid type.

Discussion.—*Orthoretiolites* may be distinguished from the Upper Ordovician genus *Archiretiolites* Eisenack (1935) in that the latter has only the sicula and initial bud with continuous periderm, the rhabdosome is represented by a reticula and the clathria, the virgula is internal, and the thecae are of curved, climacograptid type. The mode of development of *Archiretiolites* is of non-septate diplograptid type, but the direction of growth of the initial portion of th 1^2 and th 2^1 is quite different from that of *Orthoretiolites* (compare text-fig. 3 with Eisenack, 1935, p. 81, text-fig. 1).

The presence of the ventral lacinia and reticula, and the absence of a well-defined clathria in *Plegmatograptus* Elles and Wood (1908, pp. 340–343, text-figs. 222–224, pl. 34, figs. 12–14), distinguish this Upper Ordovician genus from *Orthoretiolites*.

The affinites of *Orthoretiolites* are uncertain. It displays the reduction of the periderm typical of Retiolitidae. However, the shape and arrangement of the thecae, with their apertural spines, recalls *Orthograptus*. The mode of development, summarized in the thecal diagram (text-fig. 3) is like that of *Diplograptus leptotheca* and *Orthograptus apiculatus* (Bulman, 1947, p. vii, text-fig. C). On the other hand, reduction of the periderm, development of a clathria, thecae of orthograptid type with apertural spines, are all features characteristic of Glossograptidae (Bulman, 1938, pp. 78–79). The mode of development of glossograptids is poorly known, and *Orthoretiolites* lacks the ventral lacinia typical of this family. I have placed *Orthoretiolites* in the Diplograptidae, for possibly it is more closely related to *Orthograptus* and *Diplograptus* than to genera at present placed in the Retiolitidae and Glossograptidae.

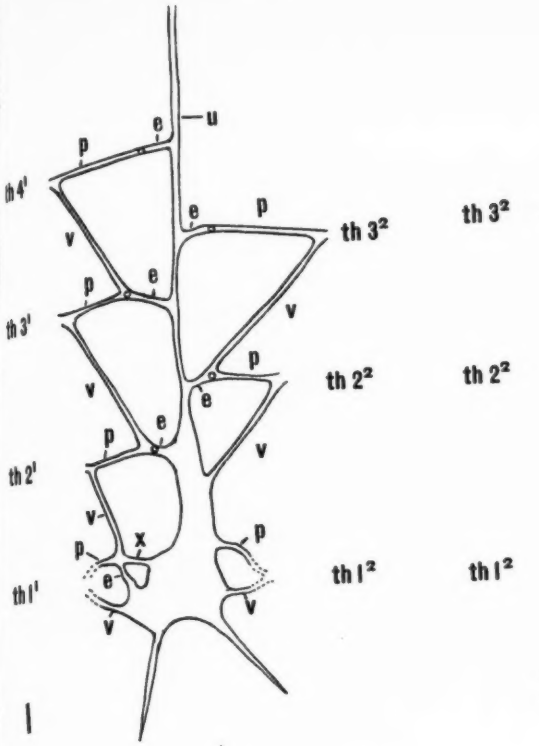
ORTHORETIOLITES HAMI Whittington, n. gen., n. sp.
Plate 63; text-figures 1–13

Material.—20 specimens, preserved in the Museum of Comparative Zoology, Harvard University (M.C.Z.) and numbered as follows: holotype, 511; other (including figured) specimens 512 a–m.

Locality and geological horizon.—The finely granular, light grey-brown limestones which yielded the graptolites were collected from 100 feet above the base of the Viola limestone in a road cut on U. S. Highway 77, centre of the E ½ sec. 25, T. 2 S., R. 1 E., Carter Co., and 2½ miles north of Springer, Oklahoma. Trilobites found here include *Cryptolithoides ulrichi* Whittington, 1941, *Robergia deckeri* Cooper, 1953, *Hypodicranotus* sp., *Trinodus* sp., and an asaphid. Graptolites yielded by dissolving the limestones include *Cryptograptus* sp., *Dicranograptus* sp., *Dicellograptus* sp., *Orthograptus* sp., *Climacograptus* aff. *C. typicalis* Hall, and three "retiolitids," one of which is the new species described herein. The trilobites suggest a Trentonian age for the beds, probably lower Trentonian, and pre-Sherman Fall age.

Description of largest rhabdosome.—Length (including virgula and virgella) approximately 3.0 mm.; width across th 1^1 and th 1^2 (excluding apertural spines) 0.8 mm.; ditto across th 4^1 and th 3^2, 1.3 mm.; sicula of length 0.9 mm. The general appearance is shown in text-figure 4, and text-figures 1 and 2 indicate the arrangement of the lists on

FIGS. *1–4*—*Orthoretiolites hami* Whittington, n. gen., n. sp. *1, 2,* Obverse and reverse lattices of the clathria respectively, showing terminology of lists and their relation to the sicula, virgula, and proximal portions of the first three thecae. Based on original of figure 4. d = dorsal list; e = parietal list; g = flange; p = pleural list; v = ventral list; u = virgula; x = additional list. Circles indicate positions of internal crossbars in the clathria; all are post-apertural lists, with the exception of the transverse list (t) associated with the lateral spine. *3,* Thecal diagram showing approximate points of origin and direction of growth of successive thecae; sicula, virgula, proximal portions of first three thecae, and reverse lattice of clathria indicated in outline only. "Common canal" in solid black. *4,* Holotype, reverse view. MCZ 511.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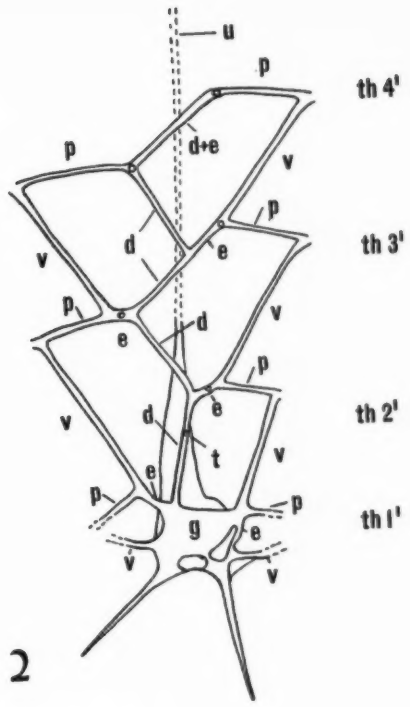
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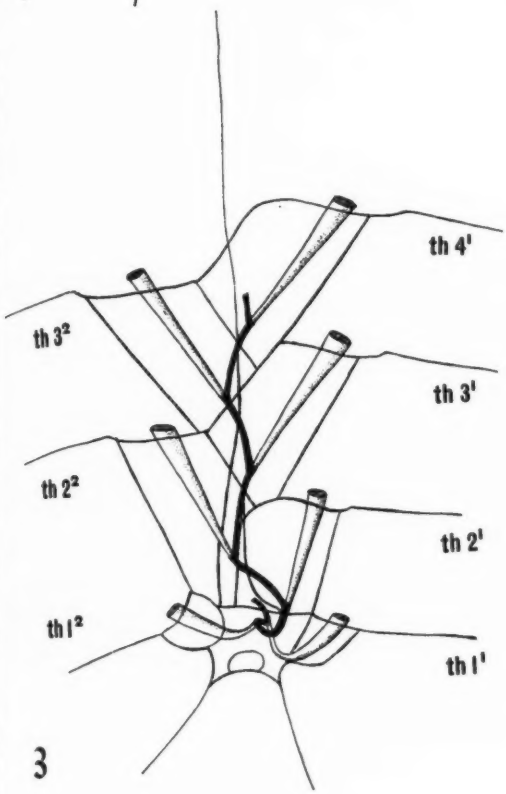
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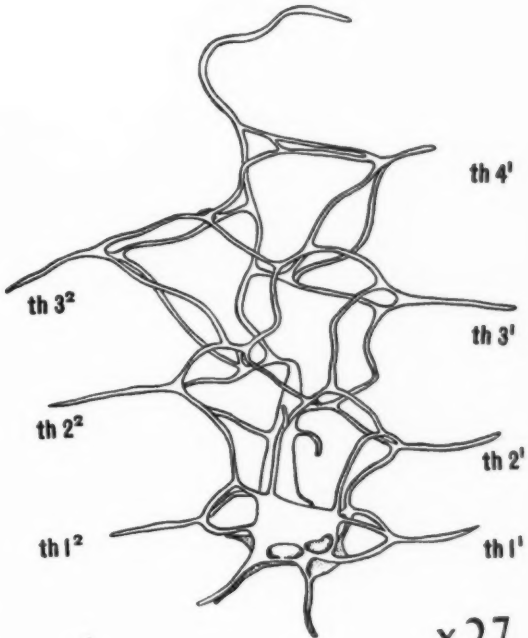
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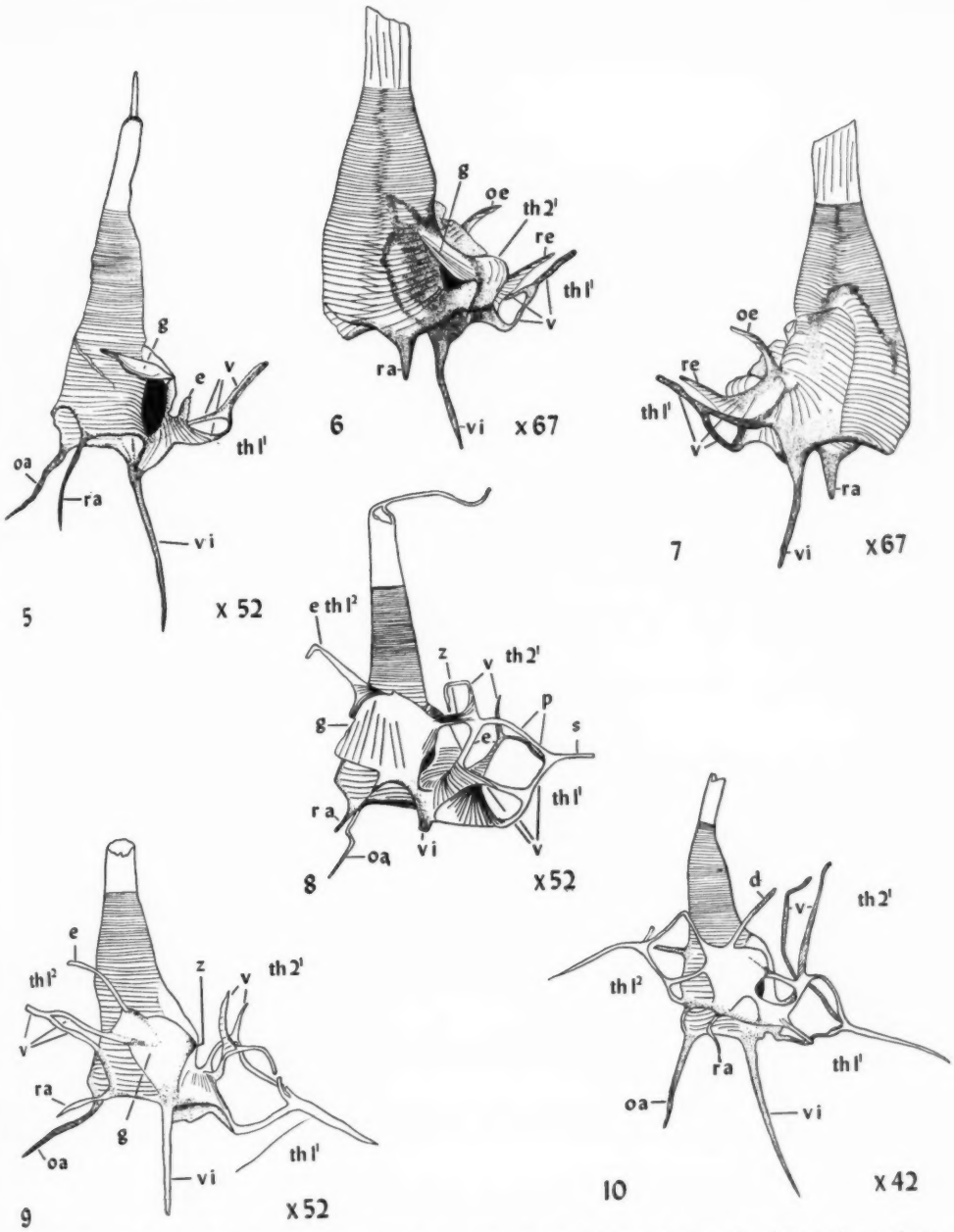
opposite sides of the clathria. Sicula with stout virgella and pair of apertural spines. Th 1^1 grows down the virgella side of the theca, turns abruptly outward so that the ventral wall is level with the sicular aperture, and then turns upwards, where the continuous periderm gives way to four lists. One pair define the ventral wall, but converge rapidly and become a single median list on the ventral wall. The second pair are parietal lists. The aperture is defined by the pleural lists, which converge outwards to meet the single ventral list. From this junction the long apertural spine arises. The distal portion of th 1^2 is of the same form and size as that of th 1^1, the ventral lists uniting distally to form a single median list. The flange (g in text-fig. 2) is a periderm sheet hanging just outside the sicula wall, the proximal (upper in text-fig. 2) edge being attached to the wall of the sicula, the distal (lower in text-fig. 2) to the outer margin of the sicula, and lists arising from the free ventral edges. The flange is the proximal part of th 1^2 and th 2^1, and the development is described below. Th 2^1 and later thecae are considerably longer and the ventral wall is defined by a pair of lists. The inner wall is defined on the reverse side (text-fig. 2) by the dorsal and parietal lists, on the obverse side (text-fig. 1) by the parietal lists and the virgula. The outer margin of the aperture is defined by the apertural list, and from the mid-point arises the long apertural spine. A post-apertural list is present in th 2^1 and later thecae. The virgula extends beyond the last-formed theca, and becomes slimmer toward the extremity. A pair of lateral spines arise at about one-third the length of the sicula. The holotype has one list on the obverse side (x in text-fig. 1) which is not seen in other specimens. A list in approximately the same situation on the reverse side is present in 512k (x in Pl. 63, fig. 4).

Discussion.—No other species that may be referred to this genus is known to me. It appears probable that the specimens figured by Ruedemann and Decker (1934, Pl. 43, figs. 18–20), and referred by them to *Lasiograptus* (*Thysanograptus*) *eucharis* (Hall), may represent the new species. They came from the same formation and the same, and adjacent, localities.

Development

The development of the first two thecae, and of the early part of the third, is shown by the specimens illustrated in Plate 63, figures 1–3, and text-figures 5–10.

Sicula and first thecae.—Two specimens, MCZ 512b and 512a, text-figs. 5–7, respective measurements in millimeters: length of prosicula 0.24, —; distal width prosicula 0.05, 0.1; length metasicula 0.65, 0.51; distal width metasicula 0.27, 0.26; length of virgella 0.37, 0.29. In 512a the distal part of the prosicula and early-formed part of the metasicula show a gradual expansion, whereas in 512b the distal part of the prosicula is cylindrical in form, and the early-formed part of the metasicula increases rapidly in width. The originals of text-figs. 8–10 show a similar variation in form of the sicula. The slim longitudinal rods of the prosicula are shown by 512a, and in all specimens the growth lines of the metasicula are close-spaced proximally, the chitin bands uniting in a zig-zag suture on opposite sides. The margin of each band is straight on antivirgella side (text-fig. 6), while proximally on the virgella side it bends slightly aperturally as the band widens (text-fig. 7). The slightness of this widening indicates that the virgella at this stage of growth was represented only by a short, blunt projection. The apertural margin of the metasicula is thickened, and there is a pair of apertural spines opposite the virgella, the margin between them deeply notched. The initial bud emerges at slightly more than half the length of the metasicula, and grows downward against the metasicula as a hood, the foramen apparently arising by resorption. As the hood (proximal portion of th 1^1) approaches the level of the sicular aperture it turns abruptly outward so that the free ventral wall of th 1^1 is level with the apertural margin of the sicula (text-fig. 7). This ventral wall is not completely sheathed with periderm, but defined by the margins of the lateral walls, which distally give rise to a pair of ventral lists. These latter curve outward and upward and unite as a single list (v in text-fig. 7). The continuous periderm of the lateral and inner walls of th 1^1 makes the abrupt right angle turn and then becomes the pair of parietal lists, the early formed portions of which are preserved in



FIGS. *5–10—Orthoretiolites hami* Whittington, n. gen., n. sp. Stages of growth of first three thecae. *5*. Oblique reverse view, th 1^1 incomplete, flange (g) representing proximal portion of th 1^2. MCZ 512b. *6*. Oblique reverse view, sicula damaged, th 1^1 incomplete, flange representing proximal portions of th 1^2 (g) and th 2^1. MCZ 512a. *7*. Oblique obverse view of same. *8*. Reverse view, th 1^1 complete, proximal portions of th 1^2 and th 2^1. MCZ 512d. *9*. Reverse view, same stage as figure 8. MCZ 512e. *10*. Reverse view, th 1^1 and th 1^2 complete, th 2^1 more advanced than figure 9. MCZ 512f. a = apertural spine of sicula; d = dorsal list; e = parietal list; g = flange; p = pleural list; s = apertural spine of theca; v = ventral list; vi = virgella; z = additional list in wall of th 2^1; o and r used as prefixes denoting obverse or reverse side of rhabdosome. Foramen of th 1^2 solid black.

512a (oe and re in text-fig. 7). On the reverse side of the hood is the ovate foramen of th 1^2 (text-figs. 5, 6). The inner edge of the foramen is slightly thickened, and chitin is added to the upper part of this edge and against the adjacent part of the sicula to form a projecting flange, lying at an angle to the growth lines of the metasicula (g in text-fig. 5). This is the early-formed part of th 1^2, that part of the "hood" proximal to it being the initial bud, the remainder of the "hood" representing the proximal portion of th 1^1. The original of text-figure 5 shows th 1^1 turning abruptly outward, and growth lines and ventral lists comparable to 512a, but only the reverse parietal list of th 1^1 appears to be developed.

Second (and initial part of third) theca.—Two specimens, MCZ 512d, 512e (text-figs. 8, 9), respective measurements (in millimeters) being: length of prosicula 0.24, ——; length of metasicula 0.58, 0.56; width at aperture 0.26, 0.24. Comparison with text-figure 6 shows that th 1^1 is completed by the growth of the pleural lists circumscribing the aperture and uniting at the outer margin with the single ventral list. From this triangular junction a thick apertural spine grows downward and outward.

Growth lines of the flange (text-figs. 5, 6, 8) suggest that growth is both downward and outward, so that the leading edge swings around until it is subparallel to the lateral margin of the sicula. In the original of text-figure 8 it is attached to the sicula near the upper edge of the foramen, and to the margin of the sicula on the reverse side near the base of the virgella and near the base of the reverse apertural spine. It lies a short distance out from the reverse side of the sicula. The upper edge of this periderm flange is thickened, and this thickened edge continued as a list, the reverse parietal list of th 1^2. In the original of text-figure 9 the reverse ventral list is proximally represented by a thickening of the periderm, and then becomes a free list. The obverse ventral list originates from the apex of the notch between the apertural spines of the sicula. Distally the two ventral lists unite and are extended upward and outward as a single list—a corresponding structure to that of th 1^1. Fragments of thin periderm lie along these and other lists, especially near junctions.

The proximal portion of th 2^1 is shown by both 512d and 512e (text-figs. 8, 9). What may be the most proximal part, however, is shown by 512a (text-fig. 6). Faint growth lines are visible, and are in a different direction (suggesting growth outward to the right in text-fig. 6) from those of the first-formed portion of the flange, which suggest growth downward (g in text-figs. 5, 6). The periderm flange thus represents not only the proximal portion of th 1^2, but also the common canal and most proximal portion of th 2^1. The ventral lists of this latter theca arise from the junctions of the parietal and pleural lists of th 1^1, and project upward. A narrow strip of thin periderm lies along the inner edge of these lists and shows growth lines. The additional list in the wall of th 2^1, which runs from the flange to the junction of the reverse parietal and pleural lists of th 1^1, is not fully developed in 512e (z in text-fig. 9) but is in 512d (z in text-fig. 8). This list is present in the originals of text-figures 10–12, but in the holotype (text-fig. 4) is represented by a broad extension of the flange.

Completion of second and third thecae.—The second theca is completed by the extension of the reverse parietal list through a right-angle to form the reverse pleural list. The obverse pleural list is curved, distally attached to the antivirgella side of the sicula level with the initial bud. The two pleural lists unite with the single ventral list, and from this three-fold junction the long apertural spine extends outward and downward. The distal portion of th 1^2 has thus the same form as that of th 1^1, and is of about the same length. Scraps of thin periderm adhere to the inner edges of the lists, particularly at the junctions.

Growth of the third theca, 2^1, is continued by (a) additions to the ventral lists so that they are sub-parallel and the distal tips somewhat below the level of the junction between pro- and metasicula; (b) the reverse dorsal list grows up from the upper edge of the periderm flange, originating close to the base of the reverse parietal list of th 1^2. At this stage (text-fig. 10, but earlier in original of text-fig. 8) the lower edge of the periderm flange is attached to the sicula at the base of the reverse apertural spine (as well as at the base of the virgella). The flange has thus a six-pointed outline, the points being where

the lists originate and the places of attachment at the lower edge. The sequence of events in the remainder of the growth of the third theca is uncertain, but the completed form is shown in text-figures 4, 11, 12. Like the later thecae, th 2^1 has paired ventral lists, an apertural list, from the center of which the apertural spine arises, and a post-apertural list. In these respects, as well as in the greater length, it differs from th 1^1 and th 1^2. In two specimens an extra list (x in Pl. 63, fig. 4; x in text-fig. 1) has been observed in th 2^1, running inward from near the base of the ventral list.

Fourth and later thecae.—The fourth theca is about the same length as the third, subsequent thecae are slightly longer. A specimen at an earlier stage than the original of text-figure 11 has the ventral lists almost complete, and a short reverse dorsal list of th 2^2, suggesting that the ventral lists are the first formed. In this specimen the post-apertural list of th 2^1 is complete. The relative positions of the lists is not exactly the same in different individuals, e.g., the position of the junction between the obverse parietal list of th 2^2 and the virgula varies, being at the apex of the sicula or a short way above it (compare text-figs. 11, 12, 13). In all the individuals shown in text-figures 4, 11–13, the obverse ventral list of th 2^2 joins the sicula wall, the position of the junction varying. In one specimen this list joins the obverse pleural list of th 1^2, and there is a short obverse parietal list of th 1^2 (e in Pl. 63, fig. 4). From this three-fold junction an additional list (y in Pl. 63, fig. 4) runs inward to the base of the reverse dorsal list of th 2^1.

During the later stages of the growth of th 2^1 a transverse list (t in text-figs. 2, 11) arises at the junction between pro- and metasicula on the reverse side. This list grows out and unites with the reverse dorsal list of th 2^1. From this point of union a long lateral spine arises (rl in text-fig. 11), thick at the base and thinning to the tip. A corresponding lateral spine arises from the opposite side of the sicula (ol in text-fig. 11). Before the fourth theca is complete, these lateral spines may have a length approximately equal to that of the metasicula. Evidently the transverse list and lateral spines may arise later in certain individuals, e. g. the original of text-figure 12, where the transverse list meets the reverse dorsal list of th 2^2.

Abnormal specimen.—The original of text-figure 13 shows peculiar features, and appears to be malformed when compared with other specimens. The sicula, initial bud with foramen, and th 1^1 appear normal except that there are two spines on the ventral wall, one below the other, the bases connected by a short list. From the base of the distal of these spines a pair of lists, probably broken, extend half-way around the margin of the theca. If these broken lists represent the margin of th 1^1, it is abnormally long, and the proximal spine cannot be apertural at this stage, but is mesial. The periderm flange is subcircular, with thickened, opaque margins, smaller than in other specimens, the lower margin farther from the level of the sicular aperture. Th 1^2 and th 2^2 are developed as in other specimens, but the theca here interpreted as being th 2^1 is displaced distally. The obverse ventral and parietal lists are attached at quite different points—the ventral to about the mid-point of the sicula, the parietal to the virgula at the apex of the sicula (compare text-figs. 12 and 13). The reverse parietal list of this theca meets the transverse list, as in other specimens, but the reverse dorsal list is missing. If the first four thecae have been correctly identified the next to appear, the fifth, is normally th 3^1, but in this specimen there is no sign of the ventral lists of th 3^1 growing up from the inner corners of the aperture of th 2^1. On the other hand, the ventral lists of th 3^2 are well-developed, and the reverse dorsal list is equally as long. The unusual position of th 2^1 thus causes the fifth theca to be th 3^2, rather than th 3^1.

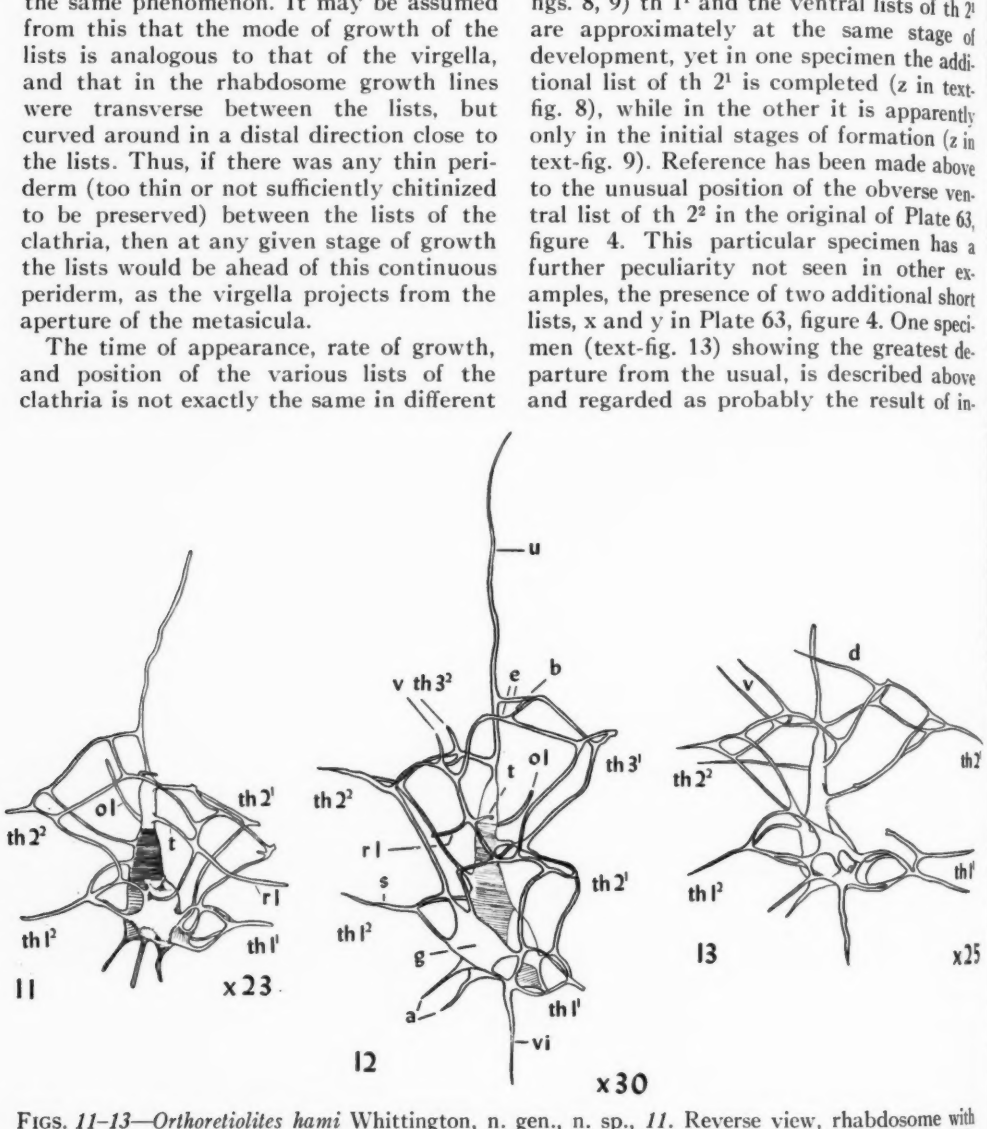
Discussion of Structure and Development

The growth bands of the metasicula (text-fig. 7; Pl. 63, figs. 2, 3) suggest that the virgella originates at approximately the same stage of growth of the metasicula as, for example, in *Archiretiolites* (Eisenack, 1935, p. 76, Pl. 4, figs. 12, 13) and *Climacograptus* (Bulman, 1947, Pl. 10, figs. 1–3).

Illustrations of metasiculae such as Bulman's (1944, p. 39) text-fig. 20 show how the growth lines swing around through nearly 90° as they approach the virgella, and become sub-parallel to it and finally merge into it. The present material, and notably the

originals of text-figures 5–10, shows that a similar swing-around of growth lines occurs close to the lists of the clathria, e.g., as the continuous periderm of the proximal portions of th 1^1 and th 1^2 gives way to a clathria. Shreds of periderm attached to later lists, particularly near junctions, show the same phenomenon. It may be assumed from this that the mode of growth of the lists is analogous to that of the virgella, and that in the rhabdosome growth lines were transverse between the lists, but curved around in a distal direction close to the lists. Thus, if there was any thin periderm (too thin or not sufficiently chitinized to be preserved) between the lists of the clathria, then at any given stage of growth the lists would be ahead of this continuous periderm, as the virgella projects from the aperture of the metasicula.

The time of appearance, rate of growth, and position of the various lists of the clathria is not exactly the same in different individuals. For example, when the reverse parietal list of th 1^2 is about at the same stage of development in two individuals (e in text-figs. 8, 9) the ventral lists of the same theca may not yet be apparent (text-fig. 8) or well on the way to completion (v in text-fig. 9). In these same two individuals (text-figs. 8, 9) th 1^1 and the ventral lists of th 2^1 are approximately at the same stage of development, yet in one specimen the additional list of th 2^1 is completed (z in text-fig. 8), while in the other it is apparently only in the initial stages of formation (z in text-fig. 9). Reference has been made above to the unusual position of the obverse ventral list of th 2^2 in the original of Plate 63, figure 4. This particular specimen has a further peculiarity not seen in other examples, the presence of two additional short lists, x and y in Plate 63, figure 4. One specimen (text-fig. 13) showing the greatest departure from the usual, is described above and regarded as probably the result of in-



FIGS. *11–13*—*Orthoretiolites hami* Whittington, n. gen., n. sp., *11*. Reverse view, rhabdosome with four complete thecae, showing transverse list (t) and reverse (r) and obverse (o) lateral spines (l). MCZ 512h. *12*. Reverse view, rhabdosome with five complete thecae, early formed part of ventral lists (v) of th 3^2. b = post-apertural list; other letters as preceding figures. MCZ 512j. *13*. Reverse view, abnormal rhabdosome with first four thecae complete, ventral (v) and dorsal (d) lists of fifth theca. MCZ 512l.

jury or other abnormality. The different position, and apparently time of development, of the transverse list in the originals of text-figures 11 and 12 has been commented on above. In one unfigured specimen, approximately at the same stage of development as the original of text-figure 10, the transverse list is present as a long, distally-tapering spine.

In diplograptids (Bulman, 1946, Pl. 4; Walker, 1953, p. 5, text-fig. 3) the foramen of th 1^2 is formed as a notch in the initial bud, chitin being laid down in strips on each side, which are united when the foramen is complete. Thus the foramen is in the wall of the initial part of th 1^2, and not adjacent to the virgella. The earliest developmental stages of *Orthoretiolites* are not available, and the foramen of th 1^2 is fully formed in the youngest individual known (text-fig. 5). The foramen is large, and one side appears to lie against the wall of the sicula. Growth lines adjacent to the outer edge of the foramen (in the initial bud and proximal part of th 1^1) cannot be made out, so the exact mode of formation of the foramen of th 1^2 remains in doubt. Further growth of th 1^2 is in the form of the flange, apparently originating at the upper edge of the foramen, extending diagonally across the foramen and upward against the wall of the sicula (g in text-fig. 5). The flange then grows downward roughly parallel to, and a short distance out from, the wall of the sicula (g in text-figs. 5, 6, 8). There do not seem to be any bands of chitin deposited at the outer, reverse margin of the sicula, extending up to meet the down-growing edge of the flange of th 1^2, as there are in typical diplograptids (e.g. Bulman, 1946, Pl. 4, figs. 3, 4; Walker, 1953, p. 7, text-fig. 5).

The thecal diagram (text-fig. 3) attempts to portray the approximate points of origin and directions of growth of successive thecae. The continuous periderm of the initial bud and proximal part of th 1^1 makes clear the direction of growth of this theca. Th 1^2 arises at about the position of the foramen, and appears to grow at first slightly upward before turning abruptly downward. The growth lines of the flange, and the clathria (text-figs. 8–10), suggest the later course of this theca. The point of origin of th 2^1 is perhaps indicated by the sharp flexure at the right-hand edge of the flange in the original of text-figure 5, and the earliest formed part of th 2^1 is preserved in the original of text-figure 6. The early course of th 2^1 is thus downward as well as outward, across the foramen, and then it curves abruptly upward to pass between the inner wall of the distal part of th 1^1 and the proximal part of th 1^2. The common canal of the later-formed part of the rhabdosome must be approximately enclosed by the transverse postapertural lists (text-figs. 1, 2) and the points of origin of later thecae are indicated accordingly. The general resemblance between the thecal diagram of *Orthoretiolites* and those of *Diplograptus leptotheca* and *Orthograptus apiculatus* (Bulman, 1947, p. vii, text-fig. C) has been referred to. Bulman (1946, p. 55) pointed out that in *Orthograptus apiculatus* the development of each of the first five thecae was conspicuously ahead of the developing edge of the common canal, or proximal part of the succeeding theca. This feature is shown by the fourth and fifth thecae in certain specimens of *Orthoretiolites*, e. g. text-figure 11, where th 2^2 is complete and the lists of the fifth theca have scarcely appeared; and text-figure 12, where th 3^1 is complete and the ventral lists of th 3^2 are short. It is also shown by the first theca (text-figs. 5, 6), but in 512d (text-fig. 8) th 1^1 is complete while th 1^2 and th 2^1 are in a generally comparable early stage of growth.

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LOWER CRETACEOUS MOLLUSCA FROM POINTE-À-PIERRE, TRINIDAD

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ABSTRACT—The paper describes fossil mollusca from a mass of Lower Cretaceous breccia which crops out on the foreshore at Pointe-à-Pierre, Trinidad, and is believed to have slipped from its original position in Paleocene times. The deposit is a reworked one and the fossils bear evidence of penecontemporaneous erosion. Four gastropod and about 20 pelecypod species are present. The gastropods include two new species: *Chartroniella saxorum* and *Oonia trinidadensis*. The pelecypods include several species which are found in the Lower Cretaceous of Europe and South America and suggest that the age is Barremian-Aptian. With them, however, are two species, *Neithea bellula* (Cragin) and *Gryphaea* cf. *G. corrugata* Say, indicative of a Comanche element in the assemblage.

INTRODUCTION

THIS paper describes a series of molluscan fossils collected by Dr. H. G. Kugler, consulting geologist of Trinidad Leaseholds Limited, from the foreshore at Pointe-à-Pierre, Trinidad, where they occur in a displaced mass of breccia which was termed by Dr. E. Lehner the "Remanié Bed," and as loose specimens which have been washed out of this breccia. They are of interest as constituting the largest assemblage of Lower Cretaceous invertebrates yet described from the West Indies. The specimens particularly mentioned have been presented by Dr. Kugler to the Department of Geology of the British Museum (Natural History), but duplicates have been deposited in the United States National Museum and in the Naturhistorisches Museum, Basle, Switzerland. Dr. Kugler has kindly sent notes on the deposit and a geological map of the locality from which information given below is derived.

THE FOSSILIFEROUS LOWER CRETACEOUS ROCKS AT POINTE-À-PIERRE

Wall and Sawkins (1860, p. 34) were the first to refer to the occurrence of fossils at Pointe-à-Pierre, and the exposures at this locality are represented at the bottom of their second sheet of sections. They recorded the discovery of fossils in a "single limestone," which was probably the "Stack Rock" by the present landing jetty, but specimens mentioned by Etheridge (p. 162) in his report on their fossils are not species occurring in this limestone, and must have been picked up on the beach. These specimens were a *Trigonia* identified as *T. subcrenulata* d'Orbigny (a species originally described from the Lower Cretaceous of Colombia) and a gastropod referred to the genus *Pteroceras*. They were considered to give "undoubted evidence" of the presence of Lower Cretaceous rocks.

Guppy (1863a, 1863b) dealt at greater length with fossils found at Pointe-à-Pierre, and the records of species contained in his two papers may be combined. The fossils were, he stated, all gathered on the beach and consequently much worn. The most conspicuous was a *Trigonia* which evidently belonged to the species which Etheridge had identified as *T. subcrenulata*. Others were a much worn belemnite, fragments of an oyster "somewhat like *Ostrea carinata* of the Lower Greensand," another oyster rather like the Recent *O. edulis*, a single valve of a "deeply sulcated bivalve," possibly an *Avicula*, but on the other hand very much like the South American fossil *Pecten alatus* von Buch, a possible *Plagiostoma* embedded in a calcareous nodule, and a "massive gibbous valve about 2½ ins. in length" with "some of the characters of a *Cytherea*." Gastropods found consisted of a cast "of a naticoid type" over 2 in. high, another species which was "either a *Trochus* or a *Pleurotomaria*," and a cast resembling one from South America which von Buch had figured as a *Rostellaria*. Guppy thought that the evidence supported Etheridge's view that the age of the fossils was Cretaceous. Both authors con-

sidered that the formation which was the source of the beach fossils was of the same age as beds exposed at Cumana, in Venezuela, and Etheridge (in Wall and Sawkins, 1860, p. 166) gave a list of fossils found there. The specimens studied by these workers have not been traced, but, now that Dr. Kugler's collection is available, the identity of the species mentioned by Guppy is obvious.

No further reference to fossils from Pointe-à-Pierre appears to have been published until 1922, when a work by Harris and Hodson on rudists from Trinidad included the description of *Praecaprina ? pennyi* from the Stack Rock. Its age was thought to be about Cenomanian. Other species described in this paper came from a limestone of probably the same age found along the Plum Road, in eastern Trinidad.

Two years later Newton (1924, p. 141) described a visit which he had paid to Pointe-à-Pierre in 1920. He, also, had been successful in obtaining a few fossils, which were not in situ, but occurred intermingled with ordinary beach material. He did not observe any exposure of rock from which they might have come. Three species from the locality are described in Newton's paper under the names *Lopha rectangularis* (Rœmer), *Exogyra sinuata* (J. Sowerby), and *Trigonia caudata* Agassiz.

G. D. Harris (in Waring, 1926, p. 91) reviewed existing knowledge of the Pointe-à-Pierre fossils and reproduced Newton's figures (pl. 16, figs. 1–3). He also recorded (p. 95) the discovery of Lower Cretaceous boulders with a very similar fauna along the Chert River, in eastern Trinidad. Liddle (1928, p. 436; also 1946, p. 703) mentioned having collected *Exogyra* and caprinid rudists from the Stack Rock at Pointe-à-Pierre, but the record of *Exogyra* is questionable. He applied the name "Plum Road Formation" to the earlier rudist limestones of Trinidad, including the Stack Rock limestone, and considered this formation to be equivalent to part of the El Cantil formation of northeastern Venezuela and to be of Aptian-Albian rather than of Cenomanian age.

Lehner (1935, p. 695) pointed out that the Lower Cretaceous fossils found loose on the beach at Pointe-à-Pierre had been washed out of a breccia exposed in patches on the foreshore, and that they occurred in this breccia as derived or "remanié" fossils. He therefore termed the breccia the "Remanié Bed" and thought that the rock from which the fossils were derived occurred near-by, possibly just off-shore. Dr. H. G. Kugler (1936, p. 1442) alluded to the "Remanié Bed" as an "intra-formational breccia," gave its thickness as 2 feet, and referred it, together with calcareous silts containing mudstone nodules with which it was interbedded, to the La Carrière formation.

Further rudists from Pointe-à-Pierre, collected by Dr. Kugler from an isolated limestone block, were described by Bouwman (1937, 1938) as *Sabinia kugleri* and *Kugleria macgillavryi*, and were considered to be Cenomanian in age. Hutchison (1938, p. 230) recorded the occurrence of the foraminifer *Epistomina* in the Pointe-à-Pierre "Capade Removido" (="Remanié Bed"), which he referred to the La Carrière shale horizon of the Cuche formation. Renz (1942, p. 523) also referred to this shale, with the "Remanié Bed," as belonging to the Cuche formation, and mentioned the occurrence of fossils identified as *?Hamites* sp., *Trigonia* (*Notoscabrotrigonia*) *tocaimana* Lea (determined by W. O. Dietrich), and *Exogyra* aff. *E. sinuata* (Sowerby).

In a recent letter Dr. Kugler reviews our present knowledge of the Cretaceous rocks at Pointe-à-Pierre as follows:

> The Lower Cretaceous masses at Pointe-à-Pierre are, in my opinion, nothing else but huge blocks completely surrounded by Paleocene Chaudière shales in which they slipped, and which formed the fore-deep of an advancing thrust mass composed of Lower and Upper Cretaceous. In Swiss terminology, the Paleocene of Pointe-à-Pierre is a "Wild-Flysch." Detailed mapping has disclosed large slip-masses of Cuche shales, Turonian Gautier shales and silty limestones with ammonites, Aptian belemnite marls, Cenomanian Caprinid limestones, and Upper Cretaceous Naparima Hill formation, and an isolated block of *Orbitolina* limestone, all in Chaudière shale.

Dr. Kugler describes the "Remanié Bed" itself as a slipped lenticular mass, up to 4 feet thick, of rubbly silt, with claystone nodules, nodular limestone lenses, and scattered fossils, all showing signs of attrition. The fossils do not appear to be derived from a much earlier formation, the re-sorting of the deposit which resulted in their erosion

having occurred penecontemporaneously. Several patches of the bed are seen at low water, and it is also exposed in the low cliff 100 feet northeast of the boat jetty, where the following section has been measured—

Black micaceous silty shale, with crimson clay-sandstone nodules	2 ft.
Slightly calcareous sandy silt	1 ft. 6 in.
Irregularly foliated micaceous silt, full of calcite veins	1 ft.
Dark grey micaceous silt with clay-sandstone lenses	2 ft.
"Remanié Bed," impure grey silt with crimson claystone nodules, nodular limestone lenses, and fossil shells	ca.3 ft.
Dark grey silt, full of calcite veins and films	3 ft.+

NOTES ON THE FOSSILS DESCRIBED AND THEIR GEOLOGICAL AGE

Most of the fossils which form the subject of this paper are water-worn, for, in addition to the erosion which they suffered during the penecontemporaneous re-sorting of the bed in which they occur, many have undergone further wear on the modern beach. Some, moreover, have a coating of very adherent matrix which obscures the sculpture and makes it extremely difficult to develop such features as the hinge-teeth. Some of the specimens have been crushed, and in several of the lamellibranchs, particularly those belonging to *Sphaera*, dorso-ventral compression has increased the convexity and relative elongation of the valve and the degree of incoiling of the umbo, producing the appearance of a convolute gastropod. Attempts to remove adherent matrix by chemical methods were unsuccessful.

The species described are listed below, the known geological ranges of those described previously being indicated by abbreviations (N, Neocomian; B, Barremian; Ap, Aptian; Al, Albian).

Gastropoda

Chartroniella saxorum, n.sp.
Oonia trinidadensis, n.sp.
Harpagodes sp.
Aporrhais sp.

Pelecypoda

Trigonarca ? sp.
Idonearca cf. *I. glabra* (Parkinson)
Idonearca sp.
Neithea atava (Roemer) [N, B]
Neithea bellula (Cragin) [Al]
Chlamys sp.
Prohinnites favrinus (Pictet and Roux) [Ap]
Spondylus sp.
Ctenoides sp.
Gryphaea cf. *G. corrugata* Say
Exogyra latissima (Lamarck) [N, B, Ap]
Exogyra minos (Coquand) [N]
Lopha (*Arctostrea*) *colubrina* (Lamarck) [N, B, Ap, Al etc.]
Pterotrigonia tocaimana (Lea) [Ap]
Megatrigonia (*Rutitrigonia*) *longa* (Agassiz) [N, B, Ap]
Cardita ? sp.
Sphaera corrugata J. Sowerby [N, B, Ap]
Epicyprina angulata (J. Sowerby) [N, B, Ap, Al]
"Cyprina" sp.
Ptychomya sp. A
Ptychomya sp. B
Panopea gurgitis (Brongniart) [N, B, Ap, Al]

If these fossils constituted an assemblage of contemporary forms, it may be seen that their most probable age is Barremian or Aptian. The only species which, apart from this record, appears to be known only from the Neocomian is *Exogyra minos*. *Neithea atava* has been recorded previously only from the Neocomian and Barremian, but *Prohinnites favrinus* and *Pterotrigonia tocaimana* are well-known Aptian forms. The presence of the two species recorded as *Neithea bellula* and *Gryphaea* cf. *G. corrugata* is of particular interest, as no comparable

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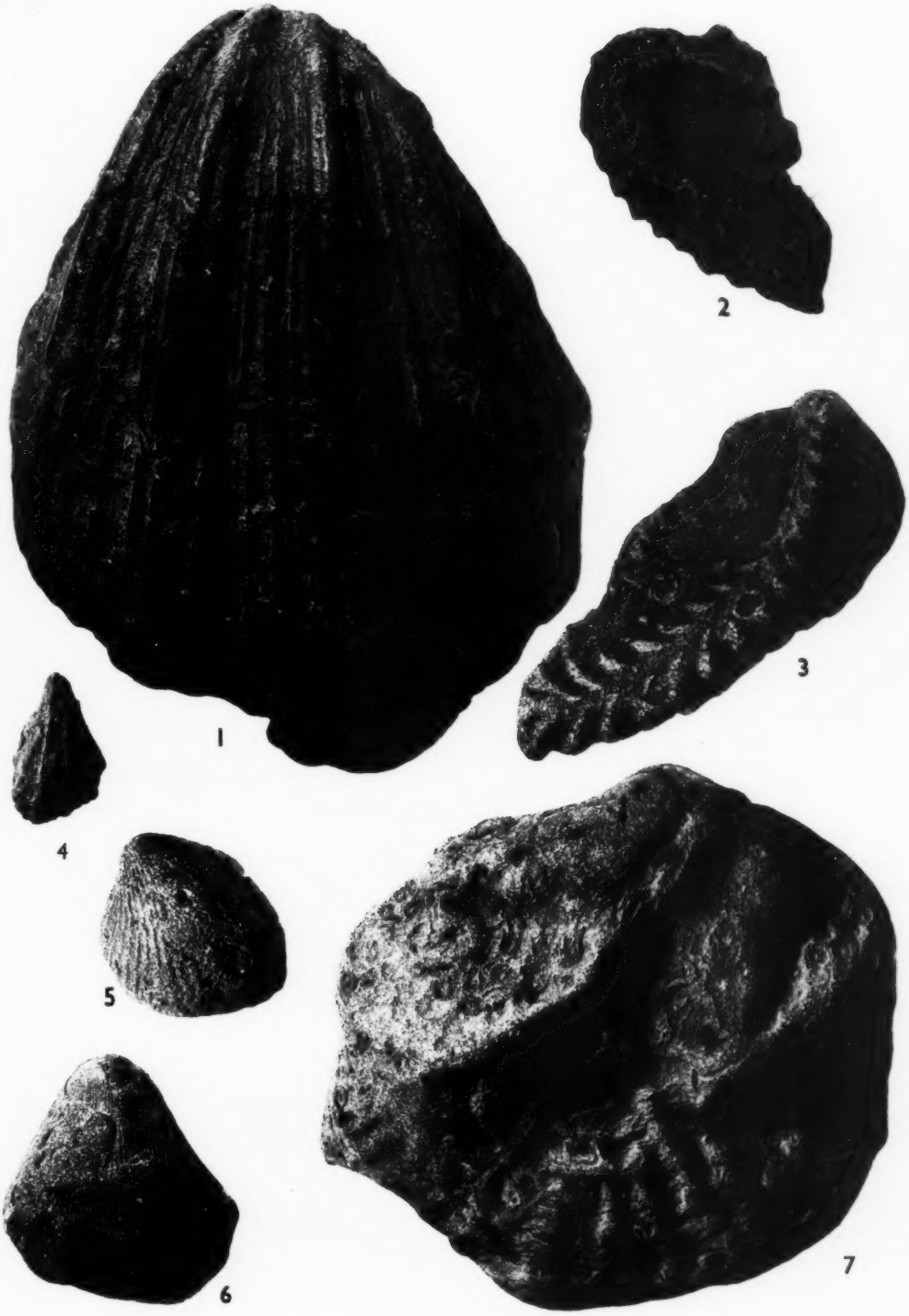
EXPLANATION OF PLATE 64

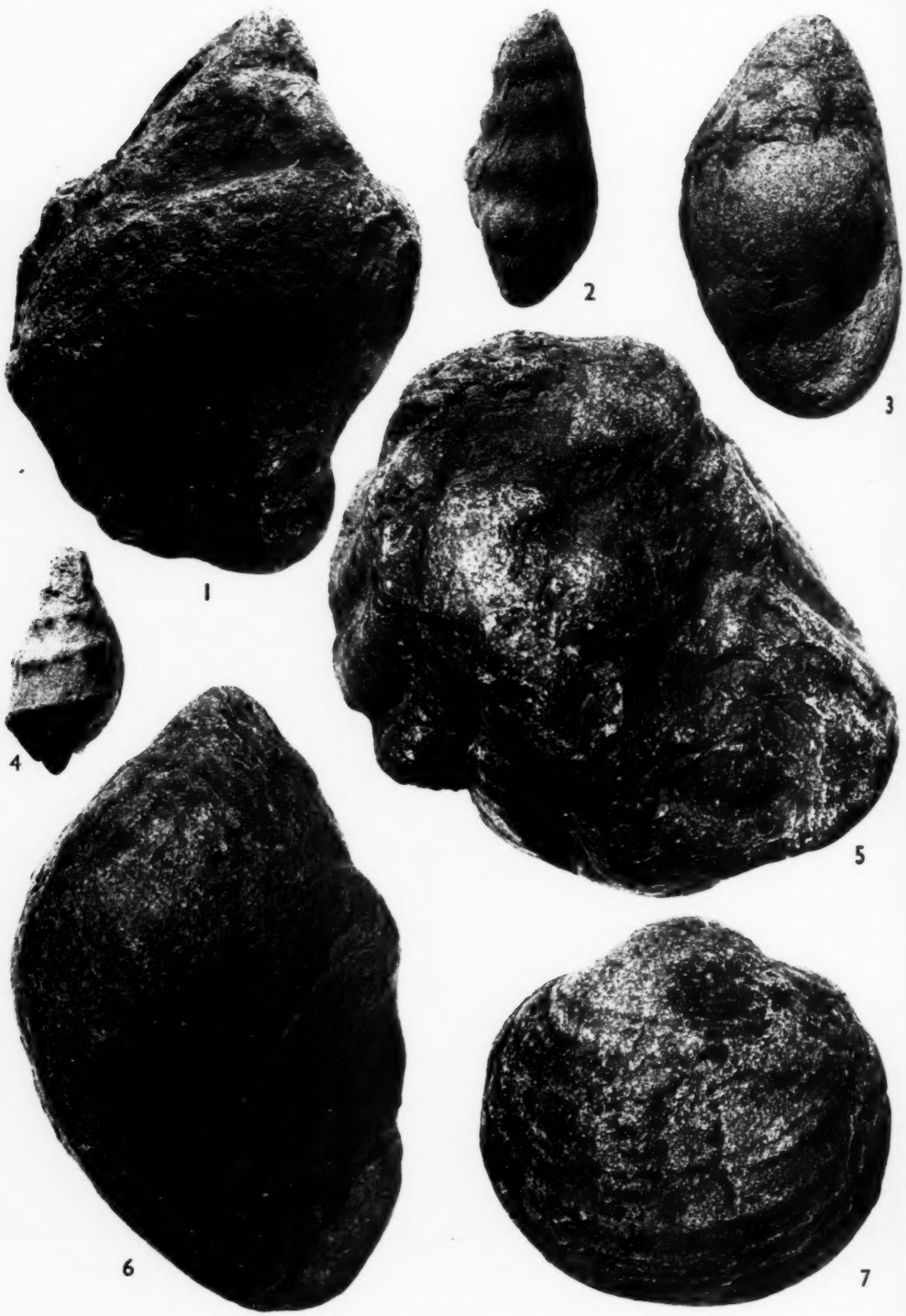
All illustrations are natural size except as noted. All specimens are from the Lower Cretaceous of Pointe-à-Pierre, Trinidad. BMGD = Geological Department of the British Museum (Natural History).

FIGS. *1, 4*—*Neithea atava* (Roemer), BMGD L.83487 and a young specimen, BMGD L.83491. (p. 627)

2, 3—*Lopha* (*Arctostrea*) *colubrina* (Lamarck), BMGD L.83529 and L.83528. (p. 630)
5—*Cardita* ? sp., BMGD L.83560. (p. 633)
6—*Neithea bellula* (Cragin), BMGD L.83495. (p. 627)
7—*Prohinnites favrinus* (Pictet & Roux), BMGD L.83497, ×⅔. (p. 628)



Cox, Trinidad Cretaceous Mollusca



Cox, Trinidad Cretaceous Mollusca

forms are known from Barremian or Aptian beds, and the species in question have been identified (in one case with the qualification "cf.") with forms which occur in the Albian Comanche series of the southern United States. Elements of the Comanche fauna seem also to be present in northeastern Venezuela, as Liddle (1946, pp. 194, 195) refers to the presence of *Gryphaea pitcheri* Morton and *G. mucronata* Gabb in this area.

The palaeontological uniformity of the whole Tethyan region, from southern Asia to the Caribbean area, in Aptian times (as, indeed, at many other times also) has been commented upon by previous workers (cf. Collet, 1922, p. 16), and is largely borne out by the assemblage of species now recorded. Familiar European species in this assemblage are *Neithea atava, Prohinnites favrinus, Exogyra minos, Lopha* (*Arctostrea*) *colubrina, Megatrigonia* (*Rutitrigonia*) *longa, Sphaera corrugata, Epicyprina angulata,* and *Panopea gurgitis,* while even *Pterotrigonia tocaimana* occurs in Europe, although it has not been known there by this name. Five of these species are also known from South America, but *N. atava, P. favrinus, L.* (*A.*) *colubrina* and *P. gurgitis* do not seem to have been recorded from that continent yet. *N. atava* and *P. gurgitis* are, however, known from the Neocomian of Mexico, while *L.* (*A.*) *colubrina* occurs in the Comanche group of the United States.

The "Remanié Bed" has yielded several species which, so far, have not been found in other areas. Unfortunately, however, most of the specimens are so eroded that, except in the case of two gastropods, it has been thought inadvisable to found new species upon them.

SYSTEMATIC DESCRIPTIONS

Class GASTROPODA

Family PARATURBINIDAE

Genus CHARTRONIELLA Cossmann, 1902

CHARTRONIELLA SAXORUM Cox, n. sp.

Plate 67, figures 2a, b, 3a, b

Trivial name.—From the Latin *saxum,* a stone, in reference to the locality Pointe-à-Pierre ("stony point").

Description.—Large for the genus, turbinate, gradate, with the height slightly exceeding the diameter. Whorls encircled by two prominent, round-topped bands, the lower of which may be overlapped until the penultimate whorl. Posterior suture bordered by a narrow, gently sloping ramp. Base strongly convex without umbilicus. Aperture suborbicular oblique.

Holotype.—BMGD[1] G.70453, measuring 31.5 mm. in height and 26 mm. in major diameter.

Remarks.—Its convex base, the absence of an umbilicus, and the two spiral bands suggest that this species should be referred to *Chartroniella,* although it is larger than Jurassic species of the genus, the type of which is a small shell from the lower Lias. The most similar described species is *Turbo faucignyanus* Pictet and Roux (1849, p. 195, pl. 19, figs. 3*a–c*), from the Albian Greensand near Geneva. In that species, however, the upper of the two spiral bands is feebly nodose, and, although all six available specimens of the species now described are eroded, it seems improbable that traces of nodes on the corresponding band have been completely removed. In *T. faucignyanus,* moreover, spiral threads are present between the bands, and the outline of the base is not so strongly convex as in the new species. Cossmann (1916, p. 39) has listed the European species under *Paraturbo,* but in the type of this genus the whorls bear very prominent, well separated, irregular nodes and have not continuous encircling bands.

[1] BMGD = Geology Department, British Museum (Natural History).

EXPLANATION OF PLATE 65

All illustrations are natural size. The specimens are all from the Lower Cretaceous of Pointe-à-Pierre, Trinidad.

FIG. *1*—*Harpagodes* sp., BMGD G.70459. (p. 626)

2, 4—*Aporrhais* sp., BMGD G.70461 and G.70462. (p. 626)

3, 6—*Oonia trinidadensis* Cox, n. sp. *3,* Paratype, BMGD G.70457; *6,* Holotype, BMGD G.70456. (p. 626)

5—*Exogyra minos* (Coquand), BMGD L.83525. (p. 630)

7—*Sphaera corrugata* J. Sowerby, BMGD L.83561. (p. 633)

Family PSEUDOMELANIIDAE
Genus OONIA Gemmellaro, 1878
OONIA TRINIDADENSIS Cox, n. sp.
Plate 65, figures 3, 6

Description. — Large, ovate-conical, smooth, without umbilicus, with a conoidal spire occupying from one-third to two-fifths of the total height. Spire whorls only of sufficient convexity to conform almost exactly to the even outline of the spire, the sutures of which are flush. Outline of last whorl of constant convexity, even to where it joins the apertural margin. Aperture narrowly pyriform. Outer lip closely adpressed posteriorly to the penultimate whorl.

Holotype.—BMGD G.70456, measuring 88 mm. in height and 59 mm. in maximum diameter.

Remarks.—This species is founded on five specimens of which the holotype is the largest. Two species described from the Lower Cretaceous of Europe are comparable in shape but do not attain nearly so large a size. These are *O. allardi* (Cossmann) (1907, p. 19, pl. 4, figs. 16–19), from the Urgonian of southern France, and *O. peroni* (Choffat) (1886, p. 24, pl. 3, figs. 5, 6), from the Valanginian of Portugal; *O. peroni* also differs in its more strongly convex whorls.

Family APORRHAIDAE
Genus HARPAGODES Gill, 1870
HARPAGODES sp.
Plate 65, figure 1

One, and probably two, imperfect specimens belong to this genus. The better one (BMGD G.70459) is 81 mm. high and has a maximum diameter of 65 mm., including incomplete remains of an expanded labrum with digitations. The spire occupies about one-third of the total height, but is too encrusted and eroded for detailed description. There were at least three conspicuous digitations, the median one of which is represented by a strong angulation, and the others by weaker angulations, on the last whorl just before it begins to expand to form the wing. There are also traces of spiral bands in the interspaces. This specimen seems to have resembled the European Valanginian species *H. desori* (Pictet and Campiche) (1864, p. 575, pl. 90, figs. 3, 4). *H. americanus* Imlay (1940, p. 158, pl. 15, fig. 9), from the Neocomian of northern Mexico, is similar in proportions, but larger.

Genus APORRHAIS da Costa, 1778
(sensu lato)
Aporrhais sp.
Plate 65, figures 2, 4

This species is represented by two imperfect specimens, in neither of which are the apertural details preserved. One (BMGD G.70461) appears to retain the remains of a short posterior digitation adhering to the spire. The original height of the larger specimen was probably about 55 mm. and that of the smaller one 33 mm. The whorl bears a row of large, prominent, rounded nodes, apparently situated on an obtuse angulation at about the middle of their height. On the smaller specimen (BMGD G.70462) the nodes are absent on the last whorl, their position being occupied by a prominent peripheral carina. Slightly below this is a well-marked although less prominent spiral cord. On the larger specimen the nodes persist as far as the broken termination of the last whorl, with the spiral cord below them.

This species appears to belong to the Aporrhaidae, but no very closely comparable Cretaceous form seems to have been described.

Class LAMELLIBRANCHIA
Family ARCIDAE
Genus TRIGONARCA Conrad, 1862
TRIGONARCA? sp.

Two much eroded specimens, showing no distinct traces of the dentition, appear from the general configuration of the shell to belong to this genus. They are about 34 mm. long and 23–24 mm. high. The umbo is broad, depressed, and slightly anterior to median, the posterior slope obtusely carinate, and the posterior end of the shell very obliquely truncated. The shape of the specimens is very similar to that of those from Zululand figured by Newton (1909, pl. 4, figs. 15, 16) as *Trigonarca ligeriensis* (d'Orbigny), but they are smaller.

Family CUCULLAEIDAE
Genus IDONEARCA Conrad, 1862
IDONEARCA cf. I. GLABRA (Parkinson)

An eroded "*Cucullaea*" 57 mm. long and 48 mm. high is not distinguishable from

specimens of the well-known European species *I. glabra*. This was originally described from the Albian Greensand of Blackdown, Devon, and specimens from the type locality have been well illustrated by Woods (1899, p. 57, pl. 11, figs. 8–12; pl. 12, figs. 1–5). In England it is confined to the Albian, but on the European continent it appears in the Aptian (Pictet and Renevier, 1857, p. 104; Pictet and Campiche, 1866, p. 456). Sommermeier (1913, p. 381) has referred to the presence of internal moulds of a comparable species in the Aptian or Albian of northern Peru. The Neocomian species *I. gabrielis* (Leymerie), which is widespread in South America, is more elongate and inequilateral, and also attains larger dimensions.

IDONEARCA sp.
Plate 66, figure 3

A second *Idonearca* has a prominent ridge on the posterior area, and therefore belongs to Mlle. Gillet's (1924, p. 16) Group 1 of representatives of the genus. The specimen (BMGD L.83486) is about 29 mm. long and 23 mm. high, with the umbo almost median and moderately prominent. *I. valdensis* (Pictet and Campiche) (1866, p. 467, pl. 131, figs. 6, 7), from the upper Gault of Switzerland, is closely comparable in the general configuration of the shell, but a little smaller. *I. bicarinata* (Coquand) (1866, p. 328, pl. 21, figs. 5, 6), from the Aptian of Spain, is larger and more inequilateral. The specimen is less elongate than the "*Cucullaea* n. sp.?" from Colombia figured by Dietrich (1938, p. 90, pl. 17, figs. 5, 6).

Family PECTINIDAE
Genus NEITHEA Drouet, 1825
NEITHEA ATAVA (Roemer)
Plate 64, figures 1, 4

Pecten atavus ROEMER, 1839, Versteinerungen des norddeutschen Oolithen-Gebirges, suppl. p. 29, pl. 18, fig. 21.
Janira atava D'ORBIGNY, 1847, Paléontologie française, Terrains crétacés, vol. 3, p. 627, pl. 442, figs. 1–3.—— PICTET & CAMPICHE, 1870, Terrain crétacé des environs de Sainte-Croix, pt. 4, p. 237, pl. 180.—— FELIX, 1891, Palaeontographica, vol. 37, p. 171.
Pecten (Neithea) atavus COSSMANN, 1907, Soc. géol. France, Mém. Paléont. no. 37, p. 37, pl. 5, fig. 19.—— COSSMANN, 1916, Soc. géol. France, Mém. Paléont. no. 51, p. 41, pl. 3, figs. 18, 19.—— COSSMANN, 1918, Soc. géol. France, Bull. ser. 4, vol. 16, p. 398, pl. 13, figs. 3–5.

The specimens (including BMGD L.83487 and L.83491) which I refer to this species are right valves in different stages of growth, the largest being over 110 mm. high and the smallest only about 20 mm. There are six main ribs, of which the four nearer the middle are very broad and are themselves divided by furrows into a broad median division and narrower lateral divisions. The main interspaces are slightly broader than these ribs, and carry three moderately strong riblets, with additional, weaker ones appearing in later growth-stages. Where the shell is uneroded, ribs and interspaces have very fine, regular, transverse threads. The largest specimens agree particularly well with the one from the upper Barremian of Brouzet-les-Alais, Gard, France, figured by Cossmann in 1907.

In the two smallest specimens (Pl. 64, fig. 4) the umbonal angle is much more acute than in the others, and it is improbable that this is entirely due to compression. Rather similar specimens have been regarded by Pictet and Campiche (1870, pl. 180, figs. 6, 7) as an early growth-stage of *N. atava*, while Roemer's original figure of this species represents a small shell not very dissimilar in shape. In these small specimens the main ribs are still simple and there are two riblets in each interspace. They also much resemble the species *N. morrisi* (Pictet and Renevier), especially as figured by Woods (1903, pl. 39, figs. 11–13) and Tavani (1948, pl. 1, figs. 10, 11). The distinctions which have been drawn between that species and small specimens of *N. atava* seem, in fact, insignificant. It is probable that the specimens which Woods (1903, pl. 39, figs. 1–5) identifies as *N. atava* and which appear so different from those which he refers to *N. morrisi* are incorrectly named, as the large, prominent anterior auricle of the right valve is not indicated in figures of the species given by other authors.

In Europe the recorded range of *N. atava* is from the Valanginian to the Barremian. Specimens which have been identified as *N. morrisi* occur in the Barremian and Aptian. Felix has recorded *N. atava* from the Neocomian of Mexico.

NEITHEA BELLULA (Cragin)
Plate 64, figure 6

Vola bellula CRAGIN, 1893, Texas Geol. Survey, 4th Ann. Rept., p. 216.

Pecten bellula ADKINS & WINTON, 1920, Texas Univ. Bull. no. 1945, p. 69, pl. 11, figs. 3–7.
Pecten (Neithea) bellulus STANTON, 1947, U.S. Geol. Survey, Prof. Paper no. 211, p. 42, pl. 42, figs. 3–7.

I refer to this species an eroded right valve (BMGD L.83495) about 35 mm. high, bearing rather more than 50 subequal narrow radial ribs. On careful examination, it can be seen that a few of these are slightly more prominent than the remainder. Both in the size and outline of the shell and in the number of ribs this specimen agrees well with the figures of *N. bellula* cited above.

According to Stanton, *N. bellula* "appears to be confined to the Fort Worth limestone and upper part of the Duck Creek limestone" at the base of the Washita group, and these formations are shown by his correlation table to be of upper Albian age. Hence the present record extends the known stratigraphical range of the species.

Hoffmann and Vadász (1913, p. 220, fig. 1) have described a middle Neocomian *Neithea* with numerous subequal ribs as a new variety *virgato-auritus* of *L. aequicostata* (Lam.), but this has a more orbicular outline than the shell now recorded and only 35 ribs.

Genus CHLAMYS Röding, 1798
CHLAMYS sp.
Plate 66, figure 5

This genus is represented by a much eroded specimen (BMGD L.83496) about 24 mm. high and 20 mm. long. It has 11 squamose radial ribs separated by interspaces of their own width.

Genus PROHINNITES Gillet, 1922
PROHINNITES FAVRINUS (Pictet and Roux)
Plate 64, figure 7

Hinnites favrinus PICTET & ROUX, 1853, Mollusques fossiles qui se trouvent dans les grès verts des environs de Genève, p. 503, pl. 43, fig. 2; pl. 44.——PICTET & CAMPICHE, 1870, Terrain crétacé des environs de Sainte-Croix, pt. 4, p. 231, pl. 178.——WOODS, 1903, Cretaceous Lamellibranchia of England vol. 1, p. 220, text-figs. 6, 7.
Prohinnites favrinus TAVANI, 1948, Palaeontologia Italica, vol. 43, p. 98, pl. 3, figs. 4, 5.

The specimens now recorded are lower valves (including BMGD L.83497), more or less orbicular in outline. The largest is about 130 mm. long. The test is very thick. Strong rounded ribs, not differing greatly in strength and crossed by the imbricating growth-layers, diverge to the lower margin from the attachment-area, which in the largest specimen occupies almost one-half of the total surface area. The specimens belong to one of several closely related species which occur in Lower Cretaceous rocks. In *Prohinnites leymerii* (Deshayes), which Weaver (1931, p. 286, pl. 29, fig. 175; pl. 30, fig. 177; pl. 31, fig. 178) has recorded from the Barremian of Argentina, the ribs are more unequal, more sparsely distributed, and mostly weaker than in the specimens now described. Rather similar differences distinguish these specimens from *P. ordonesi* Imlay (1940, p. 147, pl. 5, figs. 1, 2; pl. 6, fig. 1; pl. 7, fig. 1), from the Neocomian of northern Mexico. They appear, however, to agree well with the European Aptian species *P. favrinus*.

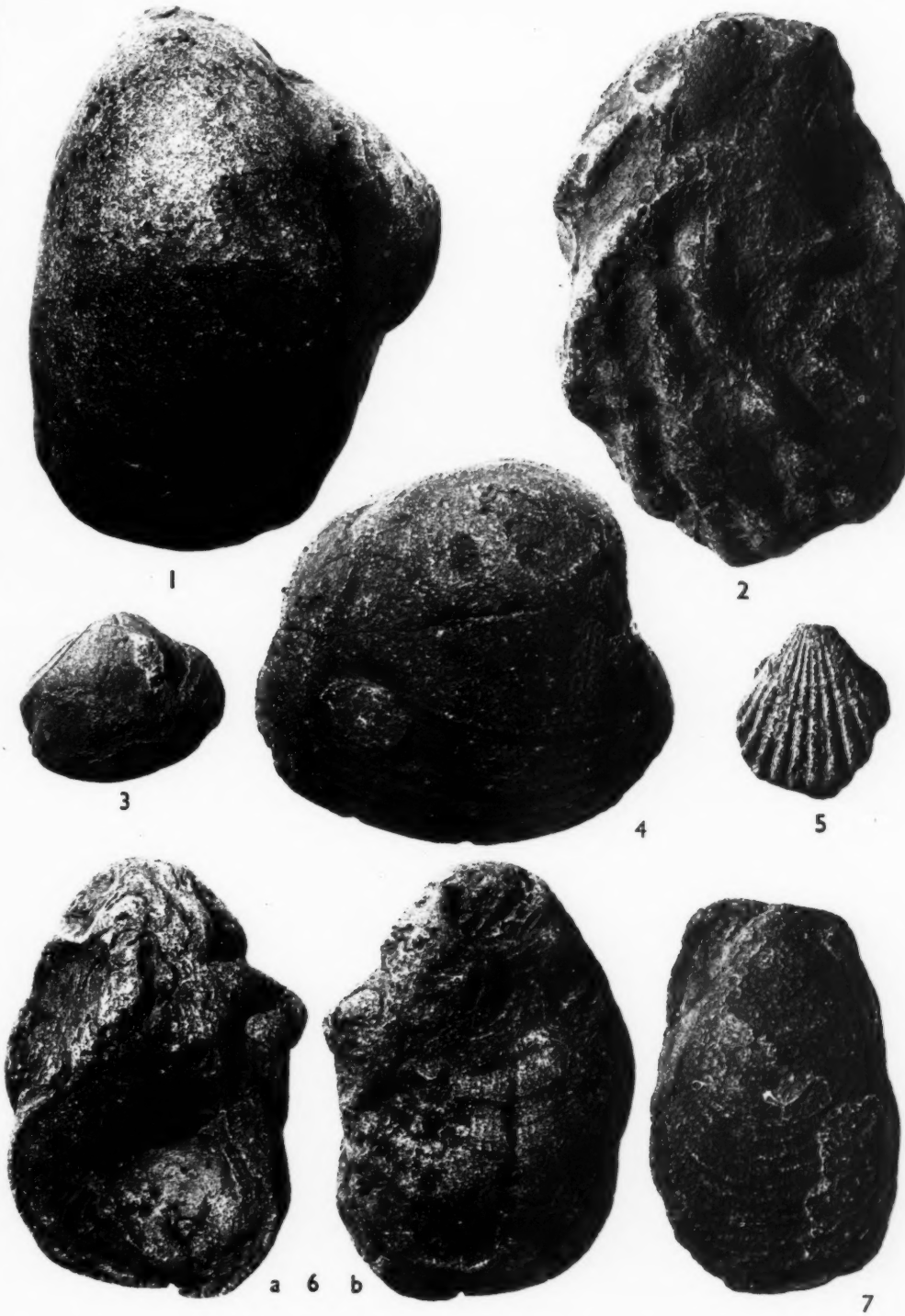
Family SPONDYLIDAE
Genus SPONDYLUS Linné, 1758
SPONDYLUS sp.
Plate 66, figures 6a, b

Two much eroded lower valves of *Spondylus* may possibly belong to the species *S. roemeri* Deshayes in Leymerie (1842, p. 10, pl. 6, figs. 8–10), which is described in most of the standard monographs on the Lower Cretaceous of Europe. They have tests of considerable thickness, and bear closely

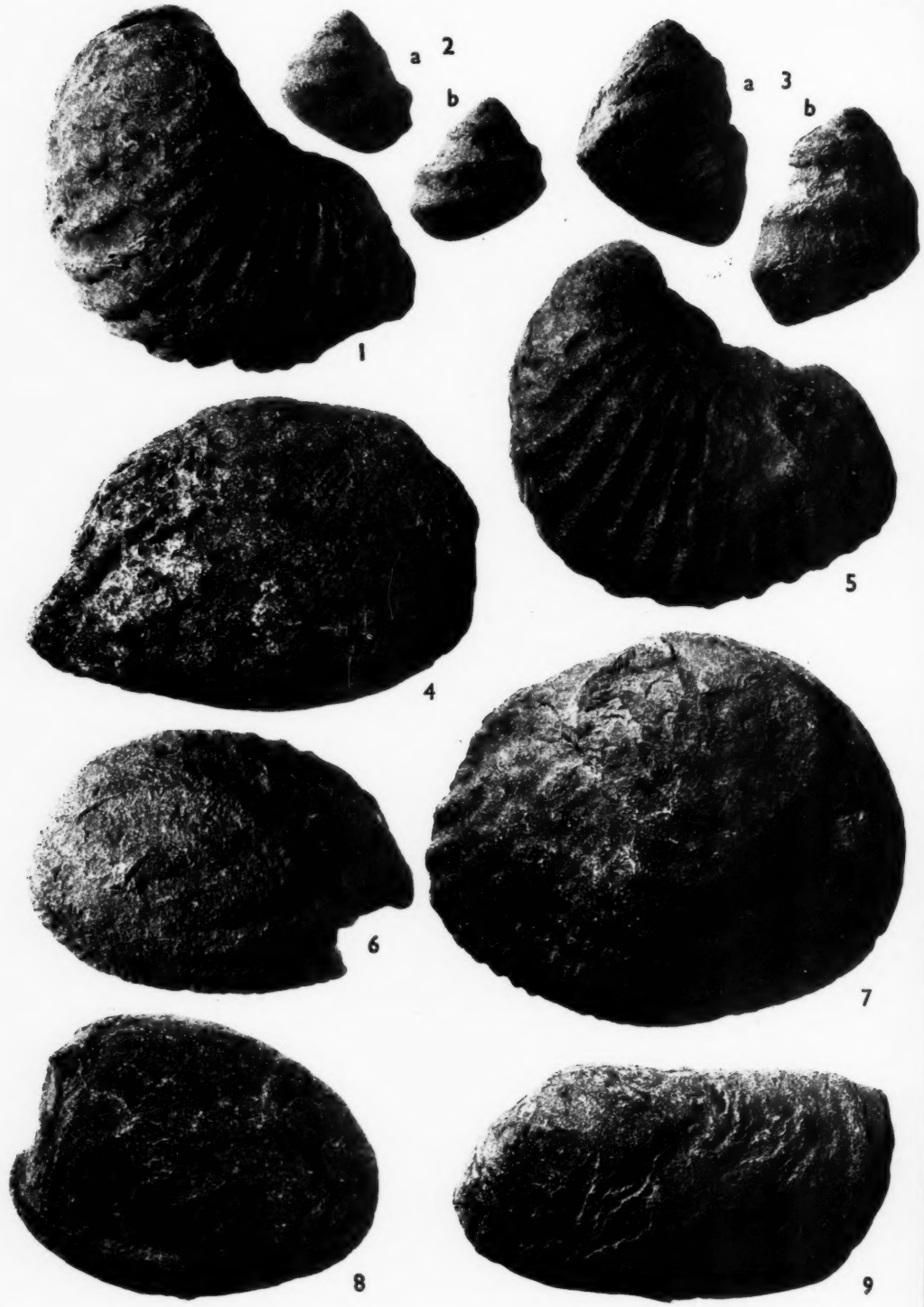
EXPLANATION OF PLATE 66

All illustrations are natural size. The specimens are all from the Lower Cretaceous of Point-à-Pierre, Trinidad.

FIG. *1*—*Gryphaea* cf. *G. corrugata* Say, BMGD L.83502. (p. 629)
2—*Exogyra minos* (Coquand), BMGD L.83526. (p. 630)
3—*Idonearca* sp., BMGD L.83486. (p. 627)
4—*Epicyprina angulata* (J. Sowerby), BMGD L.83568. (p. 633)
5—*Chlamys* sp., BMGD L.83496. (p. 628)
6a, b—*Spondylus* sp., BMGD L.83499. (p. 628)
7—*Ctenoides* sp., BMGD L.83848. (p. 629)



Cox, Trinidad Cretaceous Mollusca



Cox, Trinidad.Cretaceous Mollusca

spaced, narrow radial riblets, crossed by coarse growth-rugae. One is numbered BMGD L.83499.

Family LIMIDAE
Genus CTENOIDES Mörch, 1853
CTENOIDES sp.
Plate 66, figure 7

This genus is represented by a left valve (BMGD L.83848) 55 mm. in height, characterised by its tall, narrow, subequilateral form and feeble convexity. Up to mid-height it bears only very narrow radial threads or riblets, but in later growth-stages there are narrow, erect concentric lamellae about 2 mm. apart, with radial threads in their interspaces. No comparable member of the Limidae has been described from the Cretaceous of South America. The most similar described European species is the Urgonian *Lima essertensis* de Loriol (Pictet and Campiche, 1869, p. 139, pl. 163, figs. 7a–d), which, however, is smaller, broader and more inequilateral.

Family OSTREIDAE
Genus GRYPHAEA Lamarck, 1801
GRYPHAEA cf. G. CORRUGATA Say
Plate 66, figure 1

The genus *Gryphaea* is represented by a left valve (BMGD L.83502) 80 mm. high, 65 mm. broad, and 42 mm. deep. A posterior lobe is separated by a well-marked sulcus from the body of the valve. The lobe, as now preserved, extends ventrally for a distance equal to little more than one-half of the height of the valve, but this part of the specimen is imperfect. The specimen appears to belong to the Comanche species *G. corrugata* Say, a recent account of which has been given by Stanton (1947, p. 26, pl. 10, figs. 3–6; pl. 11, figs. 1, 3, 4). The interest of the occurrence of this *Gryphaea* at Pointe-à-Pierre is that no species of the genus of comparable size is known from pre-Comanche Cretaceous rocks, whereas all other evidence, apart from the presence of *Neithea bellula*, indicates that the assemblage now described is of pre-Comanche age. Liddle (1928, pp. 128, 131; 1946, pp. 191, 194) refers to the presence of *G. pitcheri* Morton (a synonym of *G. corrugata*), as well as of another Comanche *Gryphaea*, *G. mucronata* Gabb, in the El Cantil formation (Aptian-Albian) of northeastern Venezuela, but otherwise these Comanche gryphaeas do not appear to extend into the South American Cretaceous.

Genus EXOGYRA Say, 1820
EXOGYRA LATISSIMA (Lamarck)

Gryphaea latissima LAMARCK, 1801, Système des animaux sans vertèbres, p. 399.
Ostrea Couloni BAYLE & COQUAND, 1851, Soc. géol. France, Mém. ser. 2, vol. 4, p. 37, pl. 7, figs. 1, 2.
Exogyra aquila GERHARDT, 1897, Neues Jahrb., Beilage-Band 11, p. 175, pl. 4, fig. 10.
Exogyra Couloni BURCKHARDT, 1900, Mus. La Plata, Anales (Sec. geol. y min.), no. 2, p. 49, pl. 28, fig. 2——BURCKHARDT, 1900, Mus. La Plata, Anales (Sec. geol. y. min.), no. 3, p. 18, pl. 21, figs. 7, 8; pl. 22, fig. 3.
Exogyra aquila BURCKHARDT, 1900, idem., p. 19, pl. 22, fig. 1.
Gryphaea latissima PERVINQUIÈRE, 1910, Palaeontologia Universalis, no. 194.
Exogyra aquila SOMMERMEIER, 1913, Neues Jahrb., Beilage-Band 36, p. 391.
Exogyra sinuata WOODS, 1913, Cretaceous Lamellibranchia of England, vol. 2, p. 395, pl. 61, fig. 13; also text-figs. 194–214.
Exogyra sinuata NEWTON, 1924, Malacological Soc. London, Proc., vol. 16, p. 144, pl. 6, figs. 1, 2.——HARRIS, 1926, in Waring, Johns Hopkins Univ. Studies Geology, no. 7, p. 95, pl. 16, figs. 1, 2.
Exogyra couloni WEAVER, 1931, Univ. Washington, Mem., vol. 1, p. 229, pl. 19, figs. 88–91; also p. 228, pl. 19, figs. 93a, b (var. *leufuensis*). ——DIETRICH, 1938, Estudios geol. paleont.

EXPLANATION OF PLATE 67

All illustrations are natural size. The specimens are all from the Lower Cretaceous at Pointe-à-Pierre, Trinidad.

FIGS. *1–5*—*Pterotrigonia tocaimana* (Lea), BMGD L.83551 and L.83552. (p. 631)
2, 3—*Chartroniella saxorum* Cox, n. sp. *2a, b*, Holotype, BMGD G.70353; *3a, b*, Paratype, BMGD G.70454. (p. 625)
4, 6—*Ptychomya* species A, BMGD L.83571 and L.83572. (p. 634)
7—*Ptychomya* species B, BMGD L.83573. (p. 634)
8—"*Cyprina*" sp., BMGD L.83570. (p. 634)
9—*Panopea gurgitis* (Brongniart), BMGD L.83574. (p. 634)

Cordillera orient. Colombia, p. 87, pl. 16, figs. 1, 2.

This widespread Lower Cretaceous species is the most abundant fossil at Pointe-à-Pierre. Lamarck's name, here adopted, was published in 1801 without diagnosis but with a reference to figures in Bourguet's "Pétrifications" which, as shown by Pervinquière (1910, see synonymy), were themselves copied from Scheuchzer, who gave Neuchâtel as the locality of the figured specimens. This establishes without doubt the identity of the species intended by Lamarck, although specimens from the Lamarckian collection figured by Pervinquière do not rank as types. Names which have been used more frequently for the species are *Exogyra couloni* (Defrance), which was diagnosed but not figured in 1821, *E. sinuata* (J. Sowerby), described and well figured in 1822, and *E. aquila* (Brongniart), described and figured in the same year. Woods (1913) has given a full account of the species under Sowerby's name, so that the synonymy given above includes mainly references to records from South America. In Europe and in South America it occurs both in the Neocomian and the Aptian.

The specimens from Pointe-à-Pierre show the wide range of variation exhibited at other localities and fully illustrated by previous authors, including Woods. The largest of those which are suborbicular in outline have a diameter of about 130 mm. A narrow, transversely elongated specimen measures 180 mm. in its direction of elongation.

EXOGYRA MINOS (Coquand)
Plate 65, figure 5; plate 66, figure 2

Ostrea Boussingaultii DE LORIOL, 1861, Animaux invertébrés fossiles du Mont Salève, p. 111, pl. 14, figs. 8, 9 (*non* d'Orbigny).
Ostrea Minos COQUAND, 1869, Monographie du genre *Ostrea*, p. 183 (in part), pl. 73, figs. 5–9; pl. 74, figs. 14, 15 (non pl. 64, figs. 1–3).
Exogyra subplicata BURCKHARDT, 1900, Mus. La Plata, Anales (Sec. geol. y min.), no. 3, p. 19, pl. 22, figs. 5, 6 (non Roemer).
Ostrea minos Haupt, 1907, Neues Jahrb., Beilage-Band 23, p. 210, pl. 8, fig. 4.
Ostrea (*Exogyra*) *Minos* KRENKEL, 1910, Beiträge Paläont. Geol. Österreich-Ungarns, vol. 23, p. 206, pl. 20, fig. 4; pl. 21, fig. 7.
Exogyra Minos SOMMERMEIER, 1913, Neues Jahrb., Beilage-Band 36, p. 390, pl. 14, figs. 2, 3.
Ostrea minos WEAVER, 1931, Univ. Washington, Mem., vol. 1, p. 222, pl. 18, figs. 82, 83.
Exogyra Minos TAVANI, 1948, Palaeontologia Italica, vol. 43, p. 111, pl. 5, figs. 3, 5, 6.

Two coarsely ribbed, thick, strongly convex oyster valves (BMGD L.83525 and L.83526), the larger 85 mm. high and 75 mm. long, are referred to the species which is widespread in the Lower Cretaceous of Africa and South America and has usually been identified as *Exogyra minos*. Coquand's figures of this species consist of one set (pl. 64, figs. 1–3) copied from pl. 468 of d'Orbigny's "Paléontologie française," where they are identified as *Ostrea boussingaultii*, and of two original sets (pl. 73, figs. 5–9 and pl. 74, figs. 14, 15) illustrating specimens from France and Switzerland. The figures copied from d'Orbigny, like those of this author's (1842, p. 91, pl. 18, fig. 20; pl. 20, figs. 8, 9) original *Exogyra boussingaultii*, from the Lower Cretaceous of Colombia, represent a more regularly exogyrate and less coarsely costate oyster than those in Coquand's plates 73 and 74, to which the species *E. minos* may be restricted. *Ostrea loriolis* Coquand (1869, p. 184, pl. 73, figs. 3, 4), which de Loriol had figured in 1861 as *O. boussingaultii*, seems to be identical with the restricted *E. minos*.

Genus LOPHA Röding, 1798
Subgenus ARCTOSTREA Pervinquière, 1910
LOPHA (ARCTOSTREA) COLUBRINA (Lamarck)
Plate 64, figures 2, 3

Ostrea colubrina LAMARCK, 1819, Animaux sans Vertèbres, vol. 6, pt. 1, p. 216.——PERVINQUIÈRE, 1910, Palaeontologia Universalis, no. 198.
Ostrea diluviana WOODS, 1912, Cretaceous Lamellibranchia of England, vol. 2, p. 342, text-figs. 98–138 (non Linné).
Lopha rectangularis NEWTON, 1924, Malacological Soc. London, Proc., vol. 16, p. 143, pl. 7, figs. 1–3.
Ostrea (*Arctostrea*) *carinata* STANTON, 1947, U.S. Geol. Survey Prof. Paper 211, p. 18, pl. 7, figs. 8–13 (non Schröter, 1802).

The species now recorded is one of the most abundant at Pointe-à-Pierre, about 50 specimens (including BMGD L.83528 and L.83529) having been examined. These are narrowly lunate, up to about 80 mm. in length, subequivalve, and strongly inflated, with a series of strong costae diverg-

ing to the margins from a median crest, along which there may be a narrow space devoid of ribbing. The hinge-region may be expanded posteriorly to form a wing.

The species to which the specimens belong is the long-ranging one to which Woods applied the Linnean name *Ostrea diluviana*. The interpretation of the Linnean species has given rise to some difficulty as it was originally described without a reference to a figure, and the early Swedish authors Nilsson and Hisinger appear to differ on the subject, the former depicting a narrow, lunate form of the same general type as the specimens now recorded, and the latter a much more broadly ovate, costate form with no median ridge. I have examined the type specimen, a right valve still preserved in the Linnean Collection, and ascertained that it is a specimen of the broad form. It is deeply plicated marginally, but lacks surface costations. Woods (1912, p. 352) cites statements of Lundgren and Hennig that in Sweden the two forms are linked by specimens of an intermediate type, but when (as in the present instance) a series of numerous specimens consists entirely of the narrow, lunate form, it seems undesirable to identify the species with *O. diluviana*.

Before the appearance of the monograph by Woods, the lunate form was most frequently known as *Ostrea carinata* Lamarck or *O. frons* Parkinson. *O. carinata* (like *O. pectinata* Lamarck, also first described in 1806), was, however, a homonym of a Recent species described by Schröter in 1802, while Parkinson, when figuring a specimen as *Ostrea "frons vel folium,"* was not intending to describe a new species, but was referring to the two Linnean species *Mytilus frons* and *Ostrea folium*, both plicated Recent oysters. *Ostracites plicatissimus* Schlotheim (1813, p. 112) is said to have been the species now under discussion. It was founded without description, but with a reference to figures by Walch (1776, "Der Naturforscher," Stück 9, pl. IV, figs. 6) of an oyster, said (p. 262) to have come from Normandy, which may or may not have belonged to our species. The name does not seem to be a satisfactory one to adopt. The next name to consider is *O. colubrina* Lamarck, and as the type specimen, from the French Cenomanian, has been well illustrated by Pervinquière, there seem to be no objections to its acceptance.

Newton, in applying Roemer's name *O. rectangularis* to a specimen from Pointe-à-Pierre, was probably influenced more by its Lower Cretaceous age than by any morphological differences between it and Upper Cretaceous oysters usually known as *O. carinata*. Woods considered *O. rectangularis*, like *O. carinata*, to be a synonym of *O. diluviana*. The name *O. carinata* has been commonly used for specimens from the Comanche group of the United States (see Stanton, 1947). No comparable oyster seems to be known from the Lower Cretaceous of South America.

Family TRIGONIIDAE
Genus PTEROTRIGONIA van Hoepen, 1929
PTEROTRIGONIA TOCAIMANA (Lea)
Plate 67, figures 1, 5

Trigonia Tocaimana LEA, 1840 (July), Am. Philos. Soc., Proc., vol. 1, p. 226,

Trigonia plicato-costata NYST and GALEOTTI, 1840 (post-October), Acad. Sci. Bruxelles, Bull., vol. 7, pt. 2, p. 212, fig. 1 of pl.

Trigonia Tocaimaana LEA, 1841, Am. Philos. Soc., Trans., n. ser., vol. 7, p. 256, pl. 9, fig. 8.

Trigonia subcrenulata D'ORBIGNY, 1842, Voyage dans l'Amérique Méridionale, vol. 3, pt. 4, p. 87, pl. 19, figs. 7–9.——ETHERIDGE, 1860, in Wall and Sawkins, Geology of Trinidad, p. 162.——GERHARDT, 1897, Neues Jahrb., Beilage-Band 11, p. 184.

Trigonia crenulata var. *Peruana* PAULCKE, 1903, Neues Jahrb., Beilage-Band 17, p. 272, pl. 15, figs. 9, 9a, b.

Trigonia subcrenulata SOMMERMEIER, 1913, Neues Jahrb., Beilage-Band, 36, p. 382.——LÜTHY, 1918, Schweiz. paläont. Gesell. Abhandl. vol. 43, p. 18.

Trigonia scabricola mut. *Larteti* MUNIER-CHALMAS MS., Mengaud, 1921, Soc. Hist. nat. Toulouse, Bull. vol. 48, p. 192, pl. D, figs. 1–4.

Trigonia caudata Newton, 1924, Malacological Soc. London, Proc. vol. 16, p. 145, pl. 6, fig. 3 (non Agassiz).——HARRIS, 1926, in Waring, Johns Hopkins Univ. Studies Geology, no. 7, p. 94. pl. 16, fig. 3.

Trigonia crenulata var. *peruana* REESIDE, 1927, in Wasson and Sinclair, Am. Assoc. Petrol. Geol., Bull., vol. 11, Pt. 2, p. 1270, pl. 11, figs. 5, 6.

Trigonia subcrenulata STEINMANN, 1929, Geologie von Perú, p. 125, text-fig. 141.

Trigonia subcrenulata peruana OLSSON, 1934, Bull. Am. Paleontology, vol. 20, p. 28.

Trigonia plicatocostata MUELLERRIED, 1934, Inst. Biol. Mexico, Anales, vol. 5, p. 56, text-figs. 30–32.

Trigonia (*Notoscabrotrigonia*) *tocaimaana* DIE-

TRICH, 1938, Estudios geol. paleont. Cordillera orient. Colombia, p. 94, pl. 19, figs. 1, 2.
Trigonia subcrenulata RICHARDS, 1947, Johns Hopkins Univ. Studies Geology no. 15, p. 54, pl. 7, fig. 4.

The diagnosis of *T. tocaimana* which appeared in 1840 in the published preliminary abstract of Lea's paper, although inadequate and unaccompanied by any figure, secured priority for this name. Although it has not been pointed out previously, I am convinced that the species *T. plicato-costata*, described later in 1840 and very well illustrated by Nyst and Galeotti, was identical with Lea's species. Lea's paper, published in 1841, showed that the type of *T. tocaimana* was a broken and eroded specimen, but there is no doubt as to the identity of the species, numerous specimens of which are available in various collections. *T. tocaimana* (subsequently spelt *tocaimaana*) came from beds in Colombia (then known as New Granada) of probably Aptian age, and *T. plicato-costata* from beds in Mexico now referred to the upper Aptian (Muellerried, 1934, p. 57). Another synonym was *T. subcrenulata* d'Orbigny, based on specimens from the type-locality (Tocayma, Colombia) of *T. tocaimana*. The species is now known to occur also in Venezuela, Peru and Ecuador, usually in beds considered to be of Aptian age, although the horizon of *T. crenulata* var. *peruana* Paulcke, regarded as a further synonym, has (probably erroneously) been thought to be Turonian. Its identification in Brazil needs confirmation. The best published figures of *T. tocaimana* are those of Dietrich (1938), but the specimens illustrated are not altogether typical. I have examined several specimens of the species from Colombia and Peru in the collection of the British Museum (Natural History) and some excellent ones collected by Dr. Kugler on the island of Caribe, north of Barcelona, Venezuela, and sent to me from the collections of Trinidad Leaseholds Limited.

Specimens from Trinidad like those now under discussion were identified as *T. subcrenulata* by Etheridge (1860), but Newton (1924) accepted an opinion which Coquand had expressed that this species should be considered a synonym of *T. caudata* Agassiz, of the Lower Cretaceous of Europe. This view cannot be accepted, as in *T. caudata* the posterior extremity of the shell is more produced and tapering. In the Aptian of Spain and southern France, however, there occurs a species which appears to be identical with *T. tocaimana*. For some years this bore the manuscript name *T. larteti* Munier-Chalmas in French collections, but it was eventually described by Mengaud (1921) as *T. scabricola* mut. *larteti*. There is a very close resemblance between *T. tocaimana* and *T. scabricola* Lycett (1875, p. 130, pl. 27, figs. 4, 5), which came from the Albian Greensand of Blackdown, Devon, and if shell morphology irrespective of geological age were the criterion, it appears that *T. scabricola* would have to be relegated to the synonymy of *T. tocaimana*.

The specimens now described are about 20 in number and include BMGD L.83551 and L.83552. In the shortest the height is approximately equal to the length; one of average proportions has a height of 60 mm. and a length of 66 mm.; and the most elongate one is 51 mm. high, while its length originally exceeded 69 mm. (the posterior extremity is broken). The posterior extremity is usually relatively broad. The prominence of the umbones and the curvature of the marginal carina are variable, but in no case are the umbones so prominent as in the specimens figured by Dietrich (1938) or in the above-mentioned shells from Caribe Island, Venezuela. The tuberculate ribs descend steeply across the flank of the shell, but mostly bend in an anterior direction just before reaching its margin. Their curvature is not so strong as in several specimens in the British Museum (Natural History) from Colombia and Peru, but closely resembles that of one localized as "Angasmarcos, Peru." In no specimen is the curvature sigmoidal, as in Dietrich's plate 19, figure 2a. The narrow posterior area and the transversely ribbed escutcheon are set at an obtuse angle with the flank, and (when not eroded or obscured by a coating of matrix) are clearly visible in the side view of the shell. The variability of *T. tocaimana* has been commented upon by Richards (1947).

A discussion of the generic name *Pterotrigonia* is given in my paper on the classification of the Trigoniidae (Cox, 1952, p.

59). *T. tocaimana* is the type species of *Notoscabrotrigonia* Dietrich, which I regard as a synonym of *Pterotrigonia*.

Genus MEGATRIGONIA van Hoepen, 1929
Subgenus RUTITRIGONIA van Hoepen, 1929
MEGATRIGONIA (RUTITRIGONIA) LONGA (Agassiz)

Trigonia longa AGASSIZ, 1841, Mémoire sur les Trigonies, p. 47, pl. 8, fig. 1.
Trigonia Lajoyei DESHAYES, 1842, in Leymerie, Soc. géol. France, Mém. vol. 5, p. 7, pl. 8, fig. 4.——D'ORBIGNY, 1842, Voyage dans l'Amérique Méridionale, vol. 3, Pt. 4, p. 87, pl. 19, figs. 10, 11.
Trigonia longa D'ORBIGNY, 1844, Paléontologie française, Terrains crétacés, vol. 3, p. 130, pl. 285.——GERHARDT, 1897, Neues Jahrb., Beilage-Band 11, p. 184.——PAULCKE, 1903, Neues Jahrb., Beilage-Band 17, p. 291.——HAUPT, 1907, Neues Jahrb., Beilage-Band 23, p. 215.
——COSSMANN, 1918, Soc. géol. France, Bull., ser. 4, vol. 16, p. 411, pl. 15, figs. 12–14.
——OLSSON, 1934, Bull. Am. Paleontology, vol. 20, p. 30.——DIETRICH, 1938, Estudios geol. paleont. Cordillera orient. Colombia, p. 99.

Although broken at each end, the single specimen now recorded belongs unmistakably to this well-known species, which ranges from the Valanginian to the Aptian in Europe and has been recorded from the Lower Cretaceous of Argentina, Peru, Chile and Colombia. The names *Megatrigonia* and *Rutitrigonia* are discussed in my paper on the classification of the Trigoniidae (Cox, 1952, pp. 58, 59).

Family CARDITIDAE
Genus CARDITA Bruguière, 1792
Cardita ? sp.
Plate 64, figure 5

A much eroded, subquadrate, posteriorly subcarinate, radially ribbed left valve (BMGD L. 83560) with almost terminal umbones appears to belong to *Cardita*. It is about 26 mm. long and 25 mm. high, with an inflation of 13 mm. Owing to its worn condition the details of its ornament and dentition are not preserved. There is no described Lower Cretaceous species to which this shell could belong. *Cardita subquadrata* d'Orbigny (1843, p. 86, pl. 267, figs. 7–10) has much the same shape but is only 6 mm. long.

Family FIMBRIIDAE
Genus SPHAERA J. Sowerby, 1822
SPHAERA CORRUGATA J. Sowerby
Plate 65, figure 7

Sphaera corrugata J. Sowerby, 1822, Mineral Conchology, vol. 4, p. 42, pl. 335.
Corbis corrugata GERHARDT, 1897, Neues Jahrb., Beilage-Band 11, p. 186
Sphaera corrugata WOODS, 1907, Cretaceous Lamellibranchia of England, vol. 2, p. 157, pl. 24, fig. 24; pl. 25, figs. 1,2.
Corbis corrugata SOMMERMEIER, 1913, Neues Jahrb., Beilage-Band 36, p. 386.
Corbis (*Sphaera*) *corrugata* GILLET, 1922, Soc. Sci. Yonne, Bull., vol. 75, p. 66, pl. 3, figs. 8–10.——DIETRICH, 1938, Estudios geol. paleont. Cordillera orient. Colombia, p. 102, pl. 21, figs. 1a, b.

This well-known species, the variability of which has been discussed by Mlle. Gillet (1922), is represented by several specimens including BMGD L.83561. Some have undergone dorso-ventral compression since they were embedded, with the result that their convexity has been increased and their height diminished. In Europe this species ranges throughout the Neocomian and Aptian. Gerhardt and Dietrich have recorded it from Colombia, and Sommermeier from Peru. Imlay (1940, p. 153, pl. 7, figs. 2, 3; pl. 8, figs. 8, 9) has described a species *S. americana* from the Neocomian of Mexico which does not appear to differ from it in any features of importance.

Family CYPRINIDAE
Genus EPICYPRINA Casey, 1952
EPICYPRINA ANGULATA (J. Sowerby)
Plate 66, figure 4

Venus angulata J. Sowerby, 1814, Mineral Conchology, vol. 1, p. 145, pl. 65.
Cyprina (*Venilicardia*) *angulata* WOODS, 1907, Cretaceous Lamellibranchia of England, vol. 2, p. 141, pl. 22, figs. 1–4.
Cyprina angulata WEAVER, 1931, Univ. Washington, Mem., vol. 1, p. 325.
Epicyprina angulata CASEY, 1952, Malacological Soc. London, Proc., vol. 29, p. 154, pl. 7, fig. 2; pl. 8, fig. 1; text-figs. 72, 73.

Two right valves, the more complete of which (BMGD L.83568) is 59 mm. long and 56 mm. high, agree well with specimens of *E. angulata* from the Albian of Blackdown, the type locality of the species. Woods was of the opinion that records of the species from pre-Albian beds in England referred to distinct species, but it appears to be identified

correctly from the Aptian of France. Weaver has recorded the species from the Upper Neocomian of Argentina, and Sommermeier (1913, p. 385) has referred to the occurrence of a broken specimen, probably belonging to *E. angulata*, in the Aptian of Peru. A comparable specimen from Colombia has been figured by Dietrich (1938, p. 103, pl. 21, fig. 3) as *Cyprina* (*Venilicardia*) sp.

Genus CYPRINA Lamarck, 1818
"CYPRINA" sp.
Plate 67, figure 8

The specimen thus recorded is a highly inequilateral, ovate left valve (BMGD L.83570) 52.5 mm. long and 41 mm. high; its inflation is 17 mm. The umbo is at about the anterior eighth of the length. In a posterior direction the shell tapers very slightly to a subtruncate extremity. The hinge-teeth are too eroded for the details of their structure to be observable. The outline of the specimen is very similar to that of "*Venus*" *silvatica* Coquand (1866, p. 295, pl. 10, figs. 3, 4), from the Aptian of Spain, but that species appears to be more gibbose.

Family VENERIDAE
Genus PTYCHOMYA Agassiz, 1845
PTYCHOMYA species A
Plate 67, figures 4, 6

This species is represented by two specimens, BMGD L.83572 and L.83571, 55 mm. and just over 60 mm. long, respectively. The shell is ovate, with an oblique posterior truncation, and is less elongate than in most species of the genus, the ratio of height to length being about 2:3. The arched dorsal outline of the shell rises above the level of the umbo, which is placed at the anterior sixth of the length, and reaches its highest point at about the middle of the shell length. The posterior slope is not carinate. The smaller specimen shows the presence of backward sloping, oblique, rounded ribs which increase in amplitude posteriorly, until (as better shown in the larger specimen) those that meet the truncated posterior margin are very broad. The part of the surface anterior to the umbo has narrow, oblique ribs which slope in the opposite direction to, and form acute V's with, the main series. The dorsal margin is very coarsely crenulated, the crenulations representing the ends of a series of short, upward sloping dorsal ribs which are obscure owing to the state of preservation of the specimens. The other margins are less coarsely denticulate internally.

These specimens cannot be referred to any of the species of *Ptychomya* which have been described from South America. *P. solita* (d'Orbigny), *P. buchiana* (Karsten) and *P. koeneni* Behrendsen are more elongate and *P. lissoni* Sommermeier has different and peculiar ornament. Comparison with *P. stantoni* Cragin, from the Malone formation of Texas, is difficult as this was based on small and apparently immature specimens. The specimens from Trinidad are, however, very closely comparable in shape and ornament, to *P. zitteli* Dames (1873, p. 380, pl. 12, figs. 1, 2), from Gosau, Austria. The age of *P. zitteli* is Turonian.

PTYCHOMYA species B
Plate 67, figure 7

A much eroded right valve (BMGD L.83573) which also appears to be referable to *Ptychomya* is considerably less elongate than any described species of the genus. It is 70.5 mm. long and 55 mm. high, and is broadly ovate in outline except for an oblique posterior truncation. The ventral margin is strongly convex. The umbo is obscure, but appears to lie at about the anterior fifth of the length. As in the last species described, the dorsal margin is coarsely crenulated and the other margins are less coarsely denticulate. The posterior part of the surface has broad, oblique radial ribs. Oblique ribs, diminishing in amplitude, continue more anteriorly, but the anterior half of the surface is much worn and its ornament not visible.

Family HIATELLIDAE
Genus PANOPEA Ménard, 1807
PANOPEA GURGITIS (Brongniart)
Plate 67, figure 9

Lutraria gurgitis BRONGNIART, 1822, in Cuvier, Recherches sur les ossemens fossiles, vol. 2, Pt. 2, pp. 333, 615, pl. 9, fig. 15.
Panopea gurgitis WOODS, 1909, Cretaceous Lamellibranchia of England, vol. 2, p. 222, pl. 35, figs. 9–14, pl. 36, figs. 1–8.
Panope cf. *gurgitis* IMLAY, 1940, Geol. Soc. America, Bull., vol. 51, p. 154, pl. 6, figs. 7, 8.

A single specimen (BMGD L.83574)

about 65 mm. long, although eroded and incomplete, may be referred to this well-known Lower Cretaceous species. Weaver (1931, p. 360, pl. 41, figs. 268–270) has recorded *P. neocomiensis* (Leymerie), regarded by Woods as a synonym of *P. gurgitis*, from the Lower Cretaceous of Argentina, while Imlay's record of *P.* cf. *gurgitis* is from the Neocomian of Mexico.

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NAUTILOIDS FROM THE TANYARD FORMATION OF CENTRAL TEXAS

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ABSTRACT—This paper presents descriptions of 37 species of nautiloids from the Tanyard formation of central Texas. Of these species five are known from the Van Buren of Missouri, 20 from the Gasconade of Missouri, and seven from the Oneota of Wisconsin and Minnesota. Six of the species occur in both the Gasconade and Oneota. New species described are *Burenoceras barnesi, Conocerina cloudi, Eremoceras sansabaense, Levisoceras magnum, Walcottoceras helleri.*

INTRODUCTION

SINCE the publication of the Ozarkian-Canadian cephalopod studies of Ulrich, Foerste, Miller, and others (1942, 1943, 1944), there has accumulated a considerable nautiloid fauna from the Ozarkian beds of central Texas. These were mostly collected during the very extensive study of the Ellenburger by Cloud and Barnes. Several specimens were illustrated in their report (Cloud and Barnes, 1948), but the collections of the U. S. Geological Survey, the Texas Bureau of Economic Geology, and the University of Missouri, contain a considerable number of specimens from the Tanyard, Gorman, and Honeycut formations. In the present report those from the Tanyard are considered and they greatly strengthen the previously determined age relationships of that formation. One Gorman species is also described.

The history of stratigraphic work in the Ellenburger has been excellently described by Cloud and Barnes (1948) and need not be repeated here. It is sufficient here to point out that they used Ellenburger as a group term to include the Tanyard, Gorman, and Honeycut formations. The Tanyard is correlated with the Gasconade of Missouri, the McKenzie Hill formation of Oklahoma, and the Bliss sandstone of the trans-Pecos region of Texas. The Threadgill and Staendebach members of the Tanyard correspond respectively with the lower and upper parts of the Gasconade.

Both members of the Tanyard have yielded nautiloids at several localities. Of the species described in this report 31 occur in the Staendebach member and 10 in the Threadgill. Only three of the species are common to both members. Of the 37 species described in the present paper, five are known from the Van Buren of Missouri, 20 from the Gasconade, and seven from the Oneota of Wisconsin and Minnesota. Six of the species occur in both the Gasconade and the Oneota.

These nautiloids are preserved in chert as internal molds and it is putting it mildly to say that their preservation leaves much to be desired. However. a considerable number of them are sufficiently complete to show diagnostic generic and specific characteristics. Many fragments can be questionably identified but of course these have little stratigraphic value.

The characteristics used in classifying these chert molds are: 1) general physiognomy, including the curvature, cross-section, rate of expansion, and presence or absence of annulations; 2) nature of siphuncle, including size, cross-section shape, and position with respect to ventral wall; 3) sutures, including sinuosity, angle with long axis of shell, position and height of dorsal and ventral lobes, and depth and curvature of lateral lobes. Other features such as longitudinal striations, growth lines, or constrictions are also considered.

Arrangements for the study of this material have been made through the courtesy of Dr. Preston E. Cloud, Jr. of the U. S. Geological Survey, Dr. Virgil E. Barnes of the Texas Bureau of Economic Geology, and the late Josiah Bridge who was very much interested in this fauna. Their assistance is greatly appreciated. The material in the University of Missouri collections was collected by Dr. R. L. Heller on a private collecting trip in 1949. The study was com-

pleted under a Summer Research Fellowship of the University of Missouri Research Council, and was financially aided by Research Council Grant No. 434. I wish also to acknowledge the help of Dr. A. R. Palmer who assisted me in separating the nautiloid-bearing chert from the large amount of fossiliferous chert in the collections of the U. S. Geological Survey, and Miss Jean Berdan who supplied information concerning some of the collecting localities.

SYSTEMATIC DESCRIPTIONS

Abbreviations used in the systematic descriptions and in the plate explanations are:

USGS = United States Geological Survey
USNM = United States National Museum
TB = Texas Bureau of Economic Geology
UM = University of Missouri

Order ELLESMEROCERATIDA Flower
Family ELLESMEROCERATIDAE Kobayashi
Genus DAKEOCERAS Ulrich & Foerste, 1931
DAKEOCERAS cf. D. NORMALE Ulrich, Foerste, & Miller
Plate 70, figure 10

One small internal mold in this collection seems to be very similar to representatives of this species. This specimen is about 14 mm. long and consists of an internal mold of a living chamber with two camerae of the phragmacone. It is elliptical in cross section, being 9 mm. wide and 10 mm. high at the junction of the phragmacone and living chamber. It is gradually expanded orad.

The camerae are less than 1 mm. in length. The sutures form very shallow lateral lobes and very low dorsal and ventral saddles. The siphuncle is not preserved.

Remarks.—Although this specimen is poorly preserved it compares very favorably with the specimens referred to this species by Ulrich, Foerste, and Miller.

Occurrence.—Tanyard formation, Staendebach member, USGS loc. 28.

Repository.—USNM 123403.

DAKEOCERAS cf. D. PERRETRORSUM Ulrich, Foerste, & Miller
Plate 70, figures 1, 2

Two poorly preserved specimens in the collections of the Texas Bureau of Economic Geology appear to be similar to this species in several respects but may not actually be conspecific with it. In fact they may not actually be conspecific with each other but neither is satisfactory as a basis for a new species.

The larger of the two is an internal mold of a living chamber with portions of three camerae and part of the siphuncle attached. It is 24 mm. long and at the adapical end of the living chamber is 14 mm. wide and 16 mm. high. It is only gradually expanded orad. The cross section is broadly elliptical, nearly circular. The camerae are about 1 mm. long and the sutures are essentially straight but may have formed moderately high ventral saddles. The siphuncle is elliptical in cross section and is distinctly depressed dorso-ventrally. At the adapical end of the preserved portion it is 5 mm. wide and 3 mm. high.

The smaller specimen is also an incomplete internal mold of a living chamber which in most respects is similar to the larger one. However its sutures clearly form shallow lateral lobes and fairly high ventral saddles. The siphuncle in this specimen is also elliptical and strongly depressed dorso-ventrally.

Remarks.—The nearly circular cross section of the conch and the strong dorso-ventral depression of the siphuncle suggests that this specimen may be closely related to *D. perretrorsum* but not necessarily conspecific.

Occurrence.—Tanyard formation, Staendebach member, loc.TB 16T-2-59A.

Repository.—TB 32496 (larger specimen), 32497 (smaller specimen).

Genus BURENOCERAS Ulrich & Foerste, 1931
BURENOCERAS PUMILUM Ulrich & Foerste
Plate 68, figures 7, 8

Burenoceras pumilum ULRICH & FOERSTE, 1931, Missouri Bur. Geology and Mines, 2d ser., vol. 24, p. 208, pl. 20, figs. 32, 33.
Burenoceras pumilum ULRICH, FOERSTE, & MILLER, 1943, Geol. Soc. America, Special Paper 49, p. 64, pl. 37, figs. 18, 19.

The strong endogastric curvature of this species is well demonstrated by a small specimen from the Gorman formation of central Texas. This specimen consists of a

chert internal mold of a living chamber, two camerae, and a portion of the siphuncle.

The living chamber is about 9 mm. long and appears to be essentially complete. It is shorter than high. It is about 12 mm. high at mid-length where the width is about 9 mm. It is oval in cross section, being more broadly rounded on the dorsum than on the venter. The dorsal profile is distinctly convex, and the ventral distinctly concave.

The camerae are short, and the septa appear to have been moderately concave. The sutures are slightly sinuous and form very shallow lateral lobes and very low ventral and dorsal saddles. The siphuncle is elliptical in cross section, relatively large, and very rapidly expanded orad. The preserved portion of it is 4 mm. long and in that length it expands from a point to a height of 4 mm. and a width of 2.5 mm.

Remarks.—This specimen seems almost identical in general physiognomy with the holotype.

Occurrence.—Roubidoux zone of Ellenburger, probably Gorman formation. USGS loc. 57.

Repository.—USNM 123404.

BURENOCERAS COMPRESSSUM Ulrich, Foerste, & Miller
Plate 68, figures 5, 6

Burenoceras compressum, ULRICH, FOERSTE, & MILLER, 1943, Geol. Soc. America, Special Paper 49, p. 66, pl. 37, figs. 4, 5.

One small internal mold of a living chamber is being referred to this species, which hitherto has had only one described representative. This specimen is about 8.5 mm. long. The cross section is elliptical, and at the adapical end of the living chamber it is 5 mm. high and 3.3 mm. wide. The lateral zones flare orad and although the preservation is not good, it seems that the ventral zone was also strongly flared. The dorsal profile seems to have been slightly convex.

The sutures are essentially straight and directly transverse. The siphuncle, which is unknown in the holotype, is very small, being only 0.5 mm. in diameter at the adapical end of the living chamber. It is ventral but not quite marginal in position.

Remarks.—Despite the poor preservation of this specimen it seems clearly referable to this species.

Occurrence.—Tanyard formation, Staendebach member, USGS loc. 28.

Repository.—USNM 123405.

BURENOCERAS DICKHAUTI Ulrich, Foerste, & Miller
Plate 68, figure 15

Burenoceras dickhauti ULRICH, FOERSTE, & MILLER, 1943, Geol. Soc. America, Special Paper 49, p. 68, pl. 37, figs. 10, 11.

One small, poorly preserved chert internal mold of a living chamber is being referred to this species. It is about 9 mm. long and at the adapical end it is 9 mm. high and 7 mm. wide. The cross section is elliptical.

The septa are nearly flat and the sutures form only slight lateral lobes. The siphuncle is ventral in position and moderately large. It is about 3 mm. wide at the adapical end of the living chamber.

Remarks.—This species is very similar to *B. texanum* but has a smaller siphuncle.

Occurrence.—Tanyard formation, Threadgill member, USGS loc. TF-51.

Repository.—USNM 123406.

BURENOCERAS DILATATUM Ulrich, Foerste, & Miller
Plate 68, figure 16

Burenoceras dilatatum, ULRICH, FOERSTE, & MILLER, 1943, Geol. Soc. America, Special Paper 49, pl. 38, figs. 7, 8.

The specimen being referred to this species is a chert internal mold of a living chamber with a portion of the siphuncle and a fragment of the ventral side of the phragmacone. It appears to have been strongly curved endogastrically. The living chamber is 12.7 mm. long, and expands orad rather rapidly, especially on the ventral side which is somewhat flared. The cross section is oval, being slightly more narrowly rounded on the venter than on the dorsum. At the adapical end the living chamber is 12.5 mm. wide and about 15 mm. high.

The camerae are very short, averaging less than 1 mm. The sutures appear to have been nearly straight except for very slight ventral saddles. The siphuncle is small. It is ventral but not marginal in position.

Remarks.—This specimen is not as complete as the holotype but in all determinable characteristics it seems to be conspecific with it.

Occurrence.—Tanyard formation, Staendebach member, TB loc. 27T-9-25C.

Repository.—TB 32508.

BURENOCERAS EXPANDUM Ulrich & Foerste
Plate 68, figure 14

Burenoceras expandum ULRICH & FOERSTE, 1931, Missouri Bur. Geology Mines, 2d ser., vol. 24, p. 209, pl. 20, figs. 20, 21.
Burenoceras expandum ULRICH, FOERSTE, & MILLER, 1943, Geol. Soc. America, Special Paper, p. 69, pl. 37, figures, 20, 21.

The collections of the Texas Bureau of Economic Geology contain one small incomplete specimen that seems to belong in this species. It is a chert internal mold of a living chamber with a remnant of the siphuncle attached. This specimen is 9.5 mm. long. It is elliptical in cross section and at the adapical end is 6 mm. wide and 7.5 mm. high. The dorsal profile is convex. The ventral profile is concealed in matrix, but seems to have been concave, thus indicating an endogastric curvature. The lateral zones of the living chamber diverge strongly indicating a rather rapid orad expansion.

The adapical end is an impression of the last septum and it shows that the septa were very slightly shallowly concave, essentially plane. The suture is essentially straight and directly transverse. The siphuncle is small, circular in cross section, and ventral in position.

Remarks.—This species is characterized by the modification of the apertural margin. Although this feature is not very well preserved on this specimen it is suggested by the flaring of the living chamber.

Occurrence.—Tanyard formation. Threadgill member. TB loc. 27T-9-6C.

Repository.—TB 32507.

BURENOCERAS HUZZAHENSE Ulrich, Foerste, & Miller
Plate 68, figures 9, 10

Burenoceras huzzahense ULRICH, FOERSTE, & MILLER, 1943, Geol. Soc. America. Special Paper 49, p. 69, pl. 37, figs. 23, 24.

This species is characterized by a small subcircular conch which is not very strongly curved, and which has a small siphuncle.

The collections of the Texas Bureau of Economic Geology contain three specimens which seem to belong in this species more properly than any other. All are small chert internal molds of living chambers which range from 5 to 12 mm. in length. Two of the best specimens are illustrated but they add little or nothing to the understanding of the species. The species was originally based on only one specimen and the presently considered ones add only to the known distribution.

Occurrence.—All of these specimens are from the Tanyard formation, upper part of Staendebach member. TB loc 27T-7-56A.

Repository.—TB 32503, 32504, 32505.

BURENOCERAS TEXANUM Ulrich, Foerste, & Miller
Plate 68, figures 3, 4

Burenoceras texanum ULRICH, FOERSTE, & MILLER, 1943, Geol. Soc. America, Special Paper 49, p. 72, pl. 37, figs. 6–9.

This species seems to be represented in this collection by one very poor chert internal about 7.5 mm. long, and one mold of a living chamber with four camerae attached. The dorsal profile is moderately convex and the ventral is rather strongly concave, indicating a fairly strong endogastric curvature. The living chamber is rather rapidly expanded orad, and in the first-mentioned specimen it increases in height from about 6 mm. at the adapical end to about 10 mm. at the aperture. The cross section is elliptical, and both specimens are about 5 mm. wide at the adapical end of the living chamber.

The camerae are short. The septa were essentially flat and the sutures are nearly straight. The siphuncle is not preserved in either specimen.

Remarks.—These specimens are not identical with any of the types of this species, but in general shape and proportion they seem close enough to be regarded as conspecific.

Occurrence.—The first-mentioned specimen is from the Tanyard formation, Staendebach member, TB loc. 16T-2-59A. The other is from same member, USGS loc. B-52.

Repository.—TB 32506, USNM 123407.

BURENOCERAS UNDOSUM Ulrich, Foerste, & Miller
Plate 68, figures 1, 2

Burenoceras undosum ULRICH, FOERSTE, & MILLER, 1943, Geol. Soc. America, Special Paper 49, p. 73, pl. 37, figs. 20–22.

The collections of the University of Missouri contain a fairly complete speci-

men which seems referable to this species. It consists of an internal mold of most of a living chamber and phragmacone of which the dorsal and lateral zones are well exposed. The ventral side is concealed in the matrix. The dorsal profile is strongly convex indicating rather strong endogastric curvature. The over-all length of the specimen, measured along the dorsum, is about 30 mm. of which 11 mm. is living chamber. At the junction of the phragmacone and living chamber this specimen appears to be about 12 mm. wide and it appears to have been oval in cross section.

The camerae are short, averaging about 1 mm. The sutures are nearly straight and they slope orad from the venter to the dorsum. The siphuncle is not exposed.

One of the most distinctive characteristics of this specimen is the well developed transverse annulation of the conch. These annulations are about 2 mm. from crest to crest, and slope apicad from the venter to the dorsum, and are oblique to the sutures. They are present on both the living chamber and the phragmacone.

Remarks.—This specimen seems to be slightly larger in proportion than the holotype. However the general physiognomy and the nature of the annulations suggest a close relationship. Unfortunately the holotype did not include part of the phragmacone.

Occurrence.—Upper 75 feet of the Tanyard formation, Staendebach member. UM loc. 1.

Repository.—UM 11736.

Burenoceras barnesi Unklesbay, n. sp.
Plate 68, figures 11–13

Five specimens from the collections of the Texas Bureau of Economic Geology form the basis for this species. The one chosen as the holotype is a chert internal mold of much of a living chamber and the adoral four camerae of the phragmacone. This specimen is about 20 mm. long of which 5 mm. is the phragmacone. The dorsal profile is strongly convex and the ventral profile is concave. The living chamber is rapidly expanded orad, especially along the ventral side so that the living chamber has pitcher-spout shape. The cross section is oval, with the dorsum being more narrowly rounded than the venter. At the junction of the living chamber and phragmacone the mold is 16.5 mm. high and about 15 mm. wide.

The sutures are essentially straight and directly transverse. The camerae are short, ranging about 1 to 1.5 mm. in length.

The best of the paratypes is an internal mold of a living chamber and part of a phragmacone. It is about 28.5 mm. long, of which about half is phragmacone. Most of its ventral portion is embedded in chert matrix, but in all observable features it seems conspecific with the holotype. The two other paratypes are fragmental but seem to substantiate the need for a species to include these specimens.

Remarks.—This species is rather large for this genus. It is about the same size as the holotype of *B. peramplum* but can be differentiated from that species by the absence of annulations on the living chamber. The species name is for Dr. V. E. Barnes who has contributed so much to our understanding of the Ellenberger Group.

Occurrence.—Holotype and two of the paratypes are from the Tanyard formation, Threadgill member, TB loc. 27T-9-6A. The other two paratypes are from the Tanyard formation, Staendebach (?) member, TB loc. 27T-9-4A.

Repository.—TB, Holotype, 32498, Paratypes, 32499, 32500, 32501, 32502.

Genus Conocerina Ulrich & Foerste 1936
Conocerina missouriensis Ulrich, Foerste, & Miller
Plate 68, figures 18, 19

Conocerina missouriensis, Ulrich, Foerste, & Miller, 1943, Geol. Soc. America, Special Paper 49, pp. 104–105, pl. 52, figs. 13–14.

Only two small chert internal molds of living chambers are being referred to this species. They are smaller than the holotype, but in general shape and proportion seem more closely related to this species than to any other.

The larger specimen is about 15 mm. long. It is elliptical in cross section, being 12 mm. wide and 14 mm. high at the base of the living chamber. The dorsal side is slightly convex and the ventral side nearly straight. The septa are rather shallow and the sutures

essentially straight and directly transverse. The siphuncle is poorly preserved but apparently was small and ventral in position.

The smaller specimen is 9 mm. long. It is slightly convex along the dorsum, but nearly straight on the venter. It is elliptical in cross section and is 5.5 mm. wide and 7 mm. high at the adapical end. The septa appear to be moderately shallow and the sutures essentially straight and directly transverse. The siphuncle is very small, being only about 0.7 mm. at the adapical end of the living chamber.

Remarks.—Both of these specimens are characterized by the small siphuncle.

Occurrence.—The larger specimen is from the upper 75 feet of the Tanyard formation, Staendebach member. UM loc. 1.

The smaller specimen is from the Tanyard formation, Staendebach member, TB loc. 27T-9-46D.

Repository.—Larger specimen, UM 11737. Smaller specimen, TB 32509.

Conocerina cloudi
Unklesbay, n. sp.
Plate 68, figure 20

The holotype of this species consists of an internal mold of a nearly complete living chamber and siphuncle preserved in place in an external mold of much of the conch. This mold shows that the conch was slightly curved endogastrically, moderately expanded orad, and nearly circular in cross section.

The living chamber is 26 mm. long and near the mid-length it is 18 mm. high. A portion of the adoral camera is preserved and it indicates that the camerae were about 1 mm. long. The septa were rather deeply concave. The sutures are not well preserved but there is some indication that they were essentially straight and directly transverse. The siphuncle is large, being 6 mm. high at the junction of the phragmacone and living chamber, and is circular in cross section.

Remarks.—This species is similar in general appearance to *C. beani* but is much larger in size. It can be differentiated from other species of this genus by its relatively long living chamber, large siphuncle, and nearly circular cross section. The species name is in recognition of Dr. Preston E. Cloud, Jr.

Occurrence.—Tanyard formation, middle of Staendebach member. USGS loc. TF-110.

Holotype.—USNM 123408.

Genus Clarkoceras Ruedemann, 1905

Clarkoceras newton-winchelli
(Clarke)
Plate 69, figures 7, 8

Clarkoceras newton-winchelli Ulrich, Foerste, & Miller, 1943, Geol. Soc. America, Special Paper 49, pp. 80–81 pl. 42, figs. 1–12 (this reference contains a complete synonymy to that date).

This rather distinctive species is represented in the material being studied by two specimens. The larger of these is about 33 mm. long and consists of a chert internal mold of part of a phragmacone and living chamber. It is curved endogastrically and expands fairly rapidly orad. It is about 17 mm. wide at the junction of the phragmacone and living chamber, but the height cannot be determined because the ventral side is concealed in matrix.

The camerae are about 2 mm. long on the lateral zones. The sutures are rather strongly oblique to the long axis. They are nearly straight but because of the obliquity they form fairly prominent dorsal saddles. The siphuncle is not exposed.

The smaller specimen is very similar in general features. It is 20 mm. long, of which about half is septate.

Remarks.—Although this species has not been previously known in Texas there seems to be little question regarding the generic and specific affinity of these specimens.

Occurrence.—The larger specimen is from the Tanyard formation, Staendebach (?) member, USGS loc. TF-63, The smaller one is from the upper 75 feet of the Tanyard formation, Staendebach member, UM loc 1.

Repository.—Larger specimen USNM 123409. Smaller specimen UM 11739.

Clarkoceras arcuatum Ulrich, Foerste, & Miller
Plate 69, figure 2

Clarkoceras arcuatum Ulrich, Foerste, & Miller, 1943 Geol. Soc. America, Special Paper 49, pp. 81–82, pl. 43, figs. 11, 14, 15.

This species is represented by a poorly preserved internal mold of a latero-ventral portion of a phragmacone. The maximum length of this specimen is about 45 mm. In-

asmuch as this specimen is so incomplete the height and width cannot be reliably determined but it is estimated that the height reached about 43 mm. and the width about 25 mm. The ventral profile is slightly concave. The cross section appears to have been oval.

The camerae average about 2 mm. in length. The sutures form broad shallow lateral lobes, very low ventral saddles, and appear to have formed fairly high dorsal saddles. They are slightly oblique to the long axis of the conch. The siphuncle is not exposed.

Remarks.—This species was originally based on several fragmentary specimens. The present specimen does not add much to an understanding of the species but indicates its presence in the rocks of central Texas.

Occurrence.—Tanyard formation, near top of Staendebach member, TB loc. 16T-6-15A.

Repository.—TB 32510.

CLARKOCERAS CONFERTUM Ulrich, Foerste, & Miller
Plate 69, figures 3, 4

?Clarkoceras obliquum [nomen nudum] ULRICH, 1928. Missouri Bur. Geology Mines, 2d. ser., vol. 22, p. 68.

?Clarkoceras obliquum [nomen nudum] ULRICH, 1930, Missouri Bur. Geology Mines, 2d ser., vol. 23, p. 159.

Clarkoceras confertum ULRICH, FOERSTE, & MILLER, 1943, Geol. Soc. America, Special Paper 49, pp. 85–86, pl. 49, figs. 3, 4.

Two incomplete specimens are being referred to this species because of their apparent similarity to the holotype.

The better of the two is a chert mold of a portion of a phragmacone and a living chamber. It is rather strongly curved endogastrically, and has a concave ventral profile and convex dorsal profile. It is about 31 mm. long, of which about three-fourths is septate. The cross section is elliptical but becomes more narrowly so toward the aperture. That is, near the adapical end it is about 14 mm. high and 10 mm. wide and the lateral zones are distinctly curved; near the adoral end it is about 28 mm. high and 19 mm. wide and the lateral zones are somewhat flattened.

The camerae are short, averaging slightly more than 1 mm. The sutures form very shallow lateral lobes and are nearly straight over the venter, but they form high dorsal saddles. They become more strongly oblique adorally. The siphuncle is exposed at the adapical end and is subcircular in outline, being 3.9 mm. high and 3.2 mm. wide. It is about 1.5 mm. from the ventral wall of the conch.

The other specimen resembles this described one very closely but is less well preserved.

Remarks.—This species is very similar to *C. cuneatum* but is not as narrowly rounded on the venter.

Occurrence.—Both specimens came from the Tanyard formation, Threadgill member, TB loc. 27T-5-55B.

Repository.—TB, described specimen 32513, other specimen 32514.

CLARKOCERAS CUNEATUM Ulrich, Foerste, & Miller
Plate 69, figure 11

Clarkoceras cuneatum ULRICH, FOERSTE, & MILLER, 1943, Geol. Soc. America, Special Paper 49, p. 87, pl. 50. figs. 3–5.

Clarkoceras cuneatum CLOUD & BARNES, 1948, Univ. Texas, Publ. 4621, p. 450, pl. 39, fig. 24.

One fragmentary specimen from the Tanyard formation seems to be closely similar to the holotype of this species. It represents part of the ventral portion of a phragmacone and is about 25 mm. long. The ventral profile is concave. The camerae are about 2 mm. long and the sutures are slightly sinuous. The siphuncle is not exposed.

Occurrence.—Tanyard formation, near top of Staendebach member. TB loc. 27T-7-42A.

Repository.—TB 32512.

CLARKOCERAS HUZZAHENSE Ulrich, Foerste, & Miller
Plate 69, figure 12

Clarkoceras huzzahense ULRICH, FOERSTE, & MILLER, 1943, Geol. Soc. America, Special Paper 49, p. 90, pl. 43, figs. 9, 10.

One very fragmentary specimen in the collections being studied is referred to this species. It is an internal mold of the laterodorsal portion of a phragmacone. It is about 33 mm. long and appears to have been about 30 mm. high. The ventral profile is very slightly concave. The cross section ap-

pears to have been oval, and rather strongly compressed laterally.

The camerae average about 2 mm. in length. The sutures form fairly deep lobes on the ventro-lateral zone, rise sharply toward the dorsum, and they form fairly high ventral lobes. The siphuncle is not exposed.

Occurrence.—Tanyard formation, Staendebach member, TB loc. 16T-2-59A.

Repository.—TB 32511.

CLARKOCERAS LUTHEI (Calvin)
Plate 69, figures 9, 10

Clarkoceras luthei ULRICH, FOERSTE, & MILLER, 1943, Geol. Soc. America, Special Paper 49, pp. 93–94, pl. 47, figs. 1–11; pl. 48, figs. 1–4. (This reference contains complete synonymy to that date.)

This species, which was named a long time ago by Samuel Calvin, seems to have considerable latitude, and is here being used to include two specimens which represent different portions of the conch and which are not closely similar. However, each closely resembles forms which were referred to this species by Ulrich, Foerste, and Miller.

One of these specimens is an internal mold of a living chamber which is slightly curved endogastrically. It is about 24.5 mm. long and at the adapical end it is 13 mm. wide and 15 mm. high. The cross section is broadly oval. The rate of expansion is very slight in the adapical end of the living chamber but increases near the mid-length.

The septa are moderately deep. The sutures form broad shallow lateral lobes and fairly high rounded ventral saddles. The siphuncle is elliptical in cross section being slightly depressed dorso-ventrally. It is fairly large, being 3.5 mm. high and 5 mm. wide at the adapical end of the specimen.

The other specimen is a mold of the lateral portion of a phragmacone. It is somewhat curved and expands rather rapidly orad. It is somewhat distorted due to crushing, but the sutures appear to have been slightly sinuous and oblique to the long axis. The camerae are about 2 mm. long.

Remarks.—The first-mentioned specimen looks very much like the one illustrated by Ulrich, Foerste, and Miller in figure 1 on Plate 48. The other closely resembles the one they illustrate in figure 11 on Plate 47.

Occurrence.—Upper 75 feet of the Tanyard formation, Staendebach member. UM loc. 1.

Repository.—UM 11740, 11741.

EXPLANATION OF PLATE 68

FIGS. *1, 2—Burenoceras undosum* Ulrich, Foerste, and Miller, lateral and dorsal views, ×1½, of a specimen from the Staendebach member, UM loc. 1, UM 11736. (p. 640)

3, 4—Burenoceras texanum Ulrich, Foerste, and Miller, lateral view, ×2, of specimen from USGS loc. B-52, USNM 123407; and lateral view, ×1½, of specimen from Staendebach member, TB loc. 16T-2-59A, TB 32506. (p. 640)

5, 6—Burenoceras compressum Ulrich, Foerste, and Miller, lateral and septal views, ×3, of small specimen from Staendebach member, USGS loc 28, USNM 123405. (p. 639)

7, 8—Burenoceras pumilum Ulrich and Foerste, dorsal and lateral views of specimen from USGS loc. 57, USNM 123404. (p. 638)

9, 10—Burenoceras huzzahense Ulrich, Foerste, and Miller, lateral views, ×3, of two specimens from Staendebach member, TB loc. 27T-7-56A, TB 32503 (fig. 9), 32504 (fig. 10). (p. 640)

11, 12, 13—Burenoceras barnesi Unklesbay, n. sp., lateral view of paratype (TB 32499), lateral view of holotype (TB 32498), both from Threadgill member, and dorsal view of another paratype (TB 32501) from the Staendebach member, TB loc. 27T-9-4A. All ×1½. (p. 641)

14—Burenoceras expandum Ulrich and Foerste, lateral view of specimen, ×2, from Threadgill member, TB loc. 27T-9-6C, TB 32507. (p. 640)

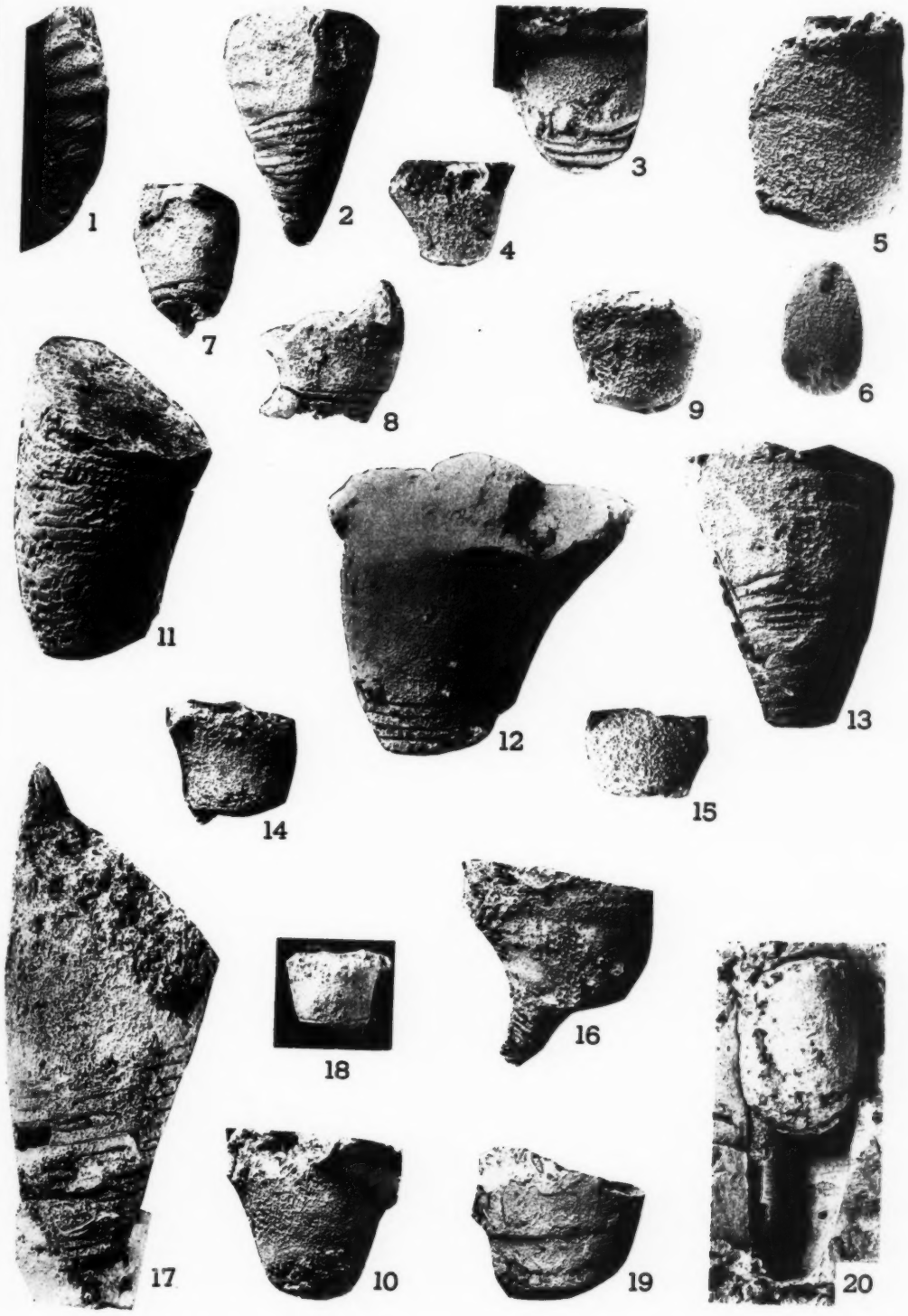
15—Burenoceras dickhauti Ulrich, Foerste, and Miller, lateral view ×2, of specimen from Tanyard formation, USGS loc. TF-51, USNM 123406. (p. 639)

16—Burenoceras dilatatum Ulrich, Foerste, and Miller, lateral view, ×1½, of specimen from Staendebach member, TB loc. 27T-9-25C, TB 32508. (p. 639)

17—Caseoceras subconicum Ulrich, Foerste, and Miller, lateral view, ×1, of specimen from Tanyard formation, USGS loc. TF-44, USNM 123411. (p. 646)

18, 19—Conocerina missouriensis Ulrich, Foerste, and Miller, lateral view, ×1½, of small specimen from Staendebach member, TB loc. 27T-9-46D, TB 32509; and lateral view ×1½ of specimen from Staendebach member UM loc. 1, UM 11737. p. (641)

20—Conocerina cloudi Unklesbay, n. sp., lateral view, ×1, of holotype, from Staendebach member, USGS loc. TF-110, USNM 123408. (p. 642)



Unklesbay, Ordovician (Tanyard) nautiloids, Texas

Unklesbay, Ordovician (Tanyard) nautiloids, Texas

CLARKOCERAS MAGNISIPHONATUM Ulrich, Foerste, & Miller
Plate 69, figure 5

Clarkoceras magnisiphonatum ULRICH, FOERSTE, & MILLER, 1943, Geol. Soc. America, Special Paper 49, p. 94, pl. 50, figs. 1, 2.

Four fragmentary specimens are being referred to this species. All are internal molds of the living chambers and siphuncle with fragments of camerae attached. Two are worthy of description.

The better of the two consists of only the adapical part of the living chamber and adoral part of the siphuncle. The cross section of the conch is oval with the venter being more narrowly rounded than the dorsum. The height of the conch is about 53 mm. and the width is about 26 mm. The camerae are short, being about 1 mm. in length. The septa are shallow. The sutures form broad shallow lateral lobes, and fairly high ventral and dorsal saddles. The ventral saddle is subangular. The large siphuncle is very distinctive. At the junction of the living chamber and phragmacone it is about 20 mm. high and 11 mm. wide. It is oval in cross section with the ventral side being more narrowly rounded than the dorsal. The surface of the siphuncle mold bears oblique annulations caused by the impression of the septal necks. The siphuncle is about 3 mm. from the ventral wall of the conch.

The other specimen is similar in almost all respects to the one described. It is a more nearly complete living chamber mold, and is about 43 mm. long. At the junction of the phragmacone and the living chamber it is about 40 mm. high and 23 mm. wide. The siphuncle is partially concealed so that exact measurements cannot be made, but it is of large proportions and is oval in cross section being compressed laterally.

Remarks.—The other two specimens being referred to this species are very poorly preserved but seem to possess most of the specific characters of the species.

Occurrence.—The first-described specimen is from the Tanyard formation, Threadgill member, USGS loc. TF-44. The second one is from the upper 75 feet of the Tanyard formation, Staendebach member, UM loc. 1. The poor specimens are from the same member at USGS loc. 28.

Repository.—USNM 123410; UM 11743.

CLARKOCERAS SUBCRASSUM Ulrich, Foerste, & Miller
Plate 69, figure 1

Clarkoceras subcrassum ULRICH, FOERSTE, & MILLER, 1943, Geol. Soc. America, Special Paper 49, pp. 98–99, pl. 51, figs. 1–4.

A very fragmentary specimen from near San Saba, Texas, is being referred to this species. It is a chert internal mold of a phragmacone, with the ventral side destroyed, and is about 40 mm. long. It is

EXPLANATION OF PLATE 69

FIGS. *1*—*Clarkoceras subcrassum* Ulrich, Foerste, and Miller, lateral view, ×1, of specimen from Staendebach member, UM loc. 1, UM 11742. (p. 645)

2—*Clarkoceras arcuatum* Ulrich, Foerste, and Miller, lateral view, ×1, of specimen from Staendebach member, TB loc. 16T-6-15A, TB 32510. (p. 642)

3, 4—*Clarkoceras confertum* Ulrich, Foerste, and Miller lateral views, ×1, of two specimens from Threadgill member, TB loc. 27T-5-55B. TB 32513 (fig. 3) and 32514 (fig. 4). (p. 643)

5—*Clarkoceras magnisiphonatum* Ulrich, Foerste, and Miller, lateral view, ×1, of specimen from Tanyard formation, USGS loc. TF-44, USNM 123410. (p. 645)

6—*Clarkoceras vicinum* Ulrich, Foerste, and Miller, lateral view, ×1½, of specimen from Staendebach member, UM loc. 1, UM 11738. (p. 646)

7, 8—*Clarkoceras newton-winchelli* (Clark), dorsal view, ×1½, of small specimen from Staendebach (?) member, USGS loc. TF-63, USNM 123409, and lateral view, ×1½, of specimen from Staendebach member UM loc. 1, UM 11739. (p. 642)

9, 10—*Clarkoceras luthei* (Calvin), lateral views of two specimens, ×1½, from the Staendebach member, UM loc. 1, UM 11740, 11741. (p 644)

11—*Clarkoceras cuneatum* Ulrich, Foerste, and Miller, lateral view, ×1, of fragmentary specimen from TB loc. 27T-7-42A, TB 32512. (p. 643)

12—*Clarkoceras huzzahense* Ulrich, Foerste, and Miller, lateral view, ×1, of specimen from Staendebach member, TB loc. 16T-2-59A, TB 32511. (p. 643)

13—*Caseoceras intermedium* Ulrich, Foerste, and Miller, lateral view of specimen from Staendebach member, UM loc. 1, UM 11744. (p. 646)

elliptical in cross section being slightly more narrowly rounded on the venter than on the dorsum. Near the mid-length of this specimen it is estimated to have been about 35 mm. high.

The camerae are about 1.5 mm. long. The sutures are strongly oblique to the long axis. They form broad shallow lateral lobes and high dorsal saddles. The siphuncle is large, being 13 mm. high and 6.5 mm. wide, and is elliptical in cross section. It appears to be orthochoanitic in structure.

Remarks.—Despite its fragmentary nature the generic and specific affinities of this specimen are clear.

Occurrence.—Upper 75 feet of the Tanyard formation, Staendebach member. UM loc. 1.

Repository.—UM 11742.

CLARKOCERAS VICINUM Ulrich, Foerste, & Miller
Plate 69, figure 6

Clarkoceras vicinum ULRICH, FOERSTE, & MILLER, 1943, Geol. Soc. America, Special Paper 49, p. 100, pl. 43, figs. 1–4.

One fragmentary specimen is being referred to this species. It consists of a chert internal mold of part of a phragmacone and siphuncle. It is about 31.5 mm. long and is septate throughout. Both the dorsal and ventral margins are nearly straight and diverge rapidly orad. The cross section is oval and changes from subcircular at the adapical end to become somewhat higher than broad toward the adoral end. Near the mid-length of the specimen the conch is 14 mm. high.

The camerae are short, being about 1.7 mm. each. The sutures are straight across the ventral and lateral zones but form fairly high rounded dorsal saddles. They are directly transverse in the adapical portion but become oblique adorally. The siphuncle is large, being about one-third as high as the conch.

Remarks.—Distinctive features of this species are its rapid expansion, its large siphuncle, and change from nearly circular to oval cross section.

Occurrence.—Upper 75 feet of the Tanyard formation, Staendebach member, UM loc. 1.

Repository.—UM 11738.

Genus CASEOCERAS Ulrich, Foerste, & Miller, 1943

CASEOCERAS INTERMEDIUM Ulrich, Foerste, & Miller
Plate 69, figure 13

Caseoceras intermedium ULRICH, FOERSTE, & MILLER, 1943, Geol. Soc. America, Special Paper 49, p. 77, pl. 40, figs. 7, 8.

Caseoceras sp. CLOUD & BARNES, 1948 [1946], Univ. Texas. Publ. 4621, pl. 39, fig. 28.

One rather incomplete specimen is being referred to this species. It is a chert internal mold of a living chamber and siphuncle to which is attached fragments of several camerae. This specimen is somewhat compressed laterally and is oval in cross section. It is about 40 mm. long, and at the junction of the living chamber and phragmacone it is estimated to have been about 34 mm. high and 20 mm. wide. The adoral portion of the living chamber appears to have had a slight constriction.

The camerae are short, averaging about 1 mm. each. The sutures are preserved on the lateral and ventral zones and here they are straight and oblique to the long axis. The siphuncle is large, being 10.5 mm. high and 6.4 mm. wide at the adapical end. It is about 4.5 mm. from the ventral wall of the conch.

Remarks.—The specimen illustrated by Cloud and Barnes and this specimen are very similar to the holotype of this species.

Occurrence.—From the upper 75 feet of Tanyard formation, Staendebach member, UM loc. 1.

Repository.—UM 11744.

CASEOCERAS SUBCONICUM Ulrich, Foerste, & Miller
Plate 68, figure 17

Caseoceras subconicum ULRICH, FOERSTE, & MILLER, 1943, Geol. Soc. America, Special Paper 49, p. 78, pl. 40, figs. 1, 2.

This species is represented in this collection by a poor but nearly complete internal mold of the phragmacone and living chamber. It is about 57 mm. long of which the adoral 24 mm. represents living chamber. The dorsal profile is nearly straight. The ventral profile is somewhat distorted in appearance by breakage of part of the living chamber. If this profile were restored it would probably be straight also. The conch

is essentially oval in cross section but is more strongly compressed in the adoral portion. It is nearly circular at the adapical end. It is rapidly expanded and increases in height from 15 mm. near the adapical end to 32 mm. near the middle of the living chamber. This is in a distance of 37 mm.

The camerae are short but increase in length from the adapical end where they are 1 mm. to the adoral part of the phragmacone where they are 2 mm. long. The sutures are straight and slightly oblique, sloping orad from the venter to the dorsum. The siphuncle is not well exposed.

Remarks.—This species is more nearly complete than the holotype of the species, but does not reveal all of the specific characters as well.

Occurrence.—Tanyard formation, Threadgill member, USGS. loc. TF-44.

Repository.—USNM 123411.

Genus ONEOTOCERAS Ulrich, 1926
ONEOTOCERAS LOCULOSUM (Hall)
Plate 70, figures 12, 13

Cyrtoceras loculosum HALL, 1861, Geol. Survey [Wis.], Rept . . . 1861, p. 42.
Cyrtoceras loculosum WHITFIELD, 1895, Am. Mus. Nat. Hist., Mem., vol. 1, pt. 2, p. 67, pl. 9, figs. 6–9.
Oneotoceras loculosum BUTTS (fide ULRICH), 1926, Ala. Geol. Survey, Special Rept. 14, pl. 15, figs. 8, 9.
"Unidentified cephalopods" POWELL, 1935, Sci. Mus. St. Paul Inst., Sci. Bull. 1, pl. 11, figs. 7, 8; pl. 12, fig. 5.
Oneotoceras loculosum STAUFFER & THIEL, 1941, Minn. Geol. Survey, Bull. 29, p. 246.
Oneotoceras loculosum ULRICH, FOERSTE, & MILLER, 1943, Geol. Soc. America, Special Paper 49, p. 145–146, pl. 65, figs. 1–3; pl. 66, figs. 6–12; pl. 67, figs. 1–10; pl. 68, figs. 13, 14.

In the collections being presently studied there is one poorly preserved specimen which is referable to this species. It is an internal mold of most of the living chamber with fragments of two camerae.

The length of the living chamber is about 15 mm. Near its mid-length it is about 19 mm. high. The lateral zones are deeply concave with the resulting groove being nearer the dorsum than the venter. The maximum width of the living chamber ventrad of the groove is 12 mm.; the width in the deepest part of the groove is 9.5 mm. and the maximum width dorsad of the groove is 10.0 mm. The crosss-section of the shell at the base of the living chamber is shown in plate 70, figure 13.

The siphuncle is small, being only 2.7 mm. in width at the base of the living chamber. It is slightly flattened laterally and is very close to the venter.

Remarks.—Despite the poor preservation of this specimen its generic and specific affinities are essentially unquestionable.

Occurrence.—Tanyard formation, probably high in Staendebach member. TB loc. no. 149T-7-15A. This species has also been reported from the Oneota dolomite of Wisconsin and Minnesota, the Gasconade dolomite of Missouri, and the Chepultepec dolomite of Tennessee.

Repository.—TB 32515.

Genus BUEHLEROCERAS Ulrich, Foerste, & Miller, 1943
BUEHLEROCERAS APERTUM Ulrich, Foerste, & Miller
Plate 71, figure 8

Buehleroceras apertum ULRICH, FOERSTE & MILLER, 1943, Geol. Soc. America, Special Paper 49, p. 61, pl. 35, figs. 9, 10; pl. 36, figs. 5, 6.

This species is represented in the collection by fragmentary chert internal molds of living chambers. This mold is about 20 mm. long and its restored width is about 13 mm. Near the apertural end, the living chamber is slightly compressed laterally causing it to contract orad, as is characteristic of this genus. The margin of the aperture has a pronounced ventral sinus with rather broadly rounded lateral salients.

As nearly as can be told from this specimen the sutures are nearly straight but form slight ventral saddles.

The siphuncle is small, laterally compressed and ventral in position.

Remarks.—In ordinary faunal studies a specimen as poor as this would probably be discarded. However the distinctive shape of the living chamber in this individual allows certain generic diagnosis, and it is the only specimen of this genus known from the Texas region.

Occurrence.—Tanyard formation, Staendebach member USGS loc. 28.

Repository.—USNM 123412.

Genus ECTENOCERAS Ulrich & Foerste, 1936

ECTENOCERAS LAQUEATUM Ulrich, Foerste, & Miller

Plate 70, figure 11

Ectenoceras laqueatum ULRICH, FOERSTE, & MILLER, 1943, Geol. Soc. America, Special Paper 49, p. 122, pl. 57, figs. 9–11.

Two fragmentary chert specimens of this species are available for study. Both are chert internal molds of the living chamber with fragments of the phragmacone attached. They are approximately the same size and in the better one the total length is 17 mm. of which 15.5 mm. represents living chamber. This specimen is about 14 mm. high and 8.5 mm. wide at the base of the living chamber. It is essentially elliptical in cross section with the lateral zones being slightly flattened. The aperture is preserved and suggests a faint flare of the shell margin with broadly rounded lateral salients and shallow ventral and dorsal sinuses.

The camerae in both specimens are very short. The sutures form broad shallow lateral lobes with low rounded saddles on the venter and dorsum. The ventral saddle rises a little higher than the dorsal.

The siphuncle is relatively large, being about 4.7 mm. in diameter at the base of the living chamber. It is close to the ventral wall.

Remarks.—These two specimens appear to have slightly shorter camerae than the holotype of the species but do not seem to merit establishment of another species.

Occurrence.—Both of these specimens came from the Tanyard formation, Staendebach member, USGS loc. 30.

Repository.—USNM 123413 (figured specimen), 123414.

Genus EREMOCERAS Hyatt, 1884

EREMOCERAS SUBRECTUM Ulrich, Foerste, & Miller

Plate 71, figures 11–13

Eremoceras subrectum, ULRICH, FOERSTE, & MILLER, 1943, Geol. Soc. America, Special Paper 49, p. 130–131, pl. 61, figs. 2–7.

One good specimen and three fragmentary ones are available for study. The best specimen is an internal mold of part of a phragmacone and is 26 mm. long. It is broadly elliptical in cross section and near the adoral end is 17.5 mm. wide. It is moderately rapid in expansion. The dorsal profile is distinctly convex and the ventral one is essentially straight.

The camerae are short, averaging about 1 mm. each. The sutures are irregular and somewhat wavy, but in general are directly transverse, except across the ventral zone where they rise slightly to form a ventral saddle. The siphuncle is ventral in position but not in contact with the shell wall. Near the adoral end of the phragmacone the siphuncle is about 2 mm. in width.

The other specimens are all internal molds of living chambers which seem to possess the characteristics of this species.

Remarks.—This species has not previously been known outside Missouri.

Occurrence.—The good specimen described above is from the upper 75 feet of the Tanyard formation, Staendebach member UM loc. 1; the Staendebach member of the Tanyard formation, TB loc. 27T-7-56A; and from the Threadgill member of the same formation, TB locs. 27T-9-46B and 27T-9-46D.

Repository.—UM 11746; TB 32517 figured specimen, 32518 and 32519 unfigured specimens.

EREMOCERAS TERES Ulrich, Foerste, & Miller

Plate 71, figures 14–17

Eremoceras teres ULRICH, FOERSTE, & MILLER, 1943, Geol. Soc. America, Special Paper 49, p 131, pl. 60, figs. 5–12.

Two fragmentary chert specimens are being referred to this species. One is an internal mold of a portion of a phragmacone about 34 mm. long. Near its mid-length it is about 18 mm. high. The other specimen is an internal mold of a nearly complete living chamber with part of the siphuncle attached. This living chamber is about 14 mm. long. The preserved portion of the apertural margin suggests the presence of a dorsal salient.

Both specimens show that the shell was curved endogastrically with the dorsal side being more strongly curved than the ventral. Both are subcircular in cross section, being very slightly compressed laterally, and in the phragmacone the conch expands orad rather gradually.

The camerae are short, being about 1.5 mm. in length, The sutures form broad fairly deep lateral lobes, a low rounded dorsal saddle, and a sub-angular ventral saddle.

The siphuncle is comparatively large for this genus. In the larger of the two specimens it is 6 mm. high where the conch is 14 mm. wide. It is depresssed and elliptical in cross section, and is near to but not in contact with the ventral wall. Oblique ridges on the siphuncle mold of the small specimen slope steeply apicad from the venter to the dorsum.

Remarks.—The suture pattern and size of the siphuncle in these two specimens seem to indicate that they are conspecific with the holotype.

Occurrence.—Tanyard formation, Threadgill member and lower Gasconade, USGS loc. B-36; Threadgill member of the Tanyard. USGS TF-41.

Repository.—USNM 123415 and 123416.

EREMOCERAS SANSABAENSE
Unklesbay, n. sp.
Plate 71, figures 9, 10

This species is being based on only one specimen which possesses the characteristics of the genus but does not seem to be conspecific with previously described species.

The holotype and only known specimen, is a chert internal mold of a living chamber, and part of the siphuncle, to which adhere portions of two camerae. This specimen is 22 mm. long. The cross section is oval, being more narrowly rounded on the venter than on the dorsum. The dorsal profile is very slightly convex and the ventral slightly concave. Near the mid-length the living chamber is 18 mm. high and 16.6 mm. wide. The apertural margin is sinuous. There is a broad dorsal salient, shallow dorso-lateral sinus, a low broad ventro-lateral salient and a fairly deep subangular ventral sinus. Faintly preserved growth lines on the adoral portion of the living chamber parallel the margin.

The sutures are essentially straight, except across the venter where they form a small subangular saddle. The siphuncle is fairly large for this genus. At the base of the living chamber it is 6 mm. wide and 5 mm. high, and is elliptical in cross section. It is ventral and marginal in position.

Remarks.—The most distinctive characteristics of this species are the size of the siphuncle and the sinuous apertural margin. The specific name is used because the holotype came from San Saba County, Texas.

Occurrence.—Tanyard formation, Staendebach member. USGS TF-37.

Holotype.—USNM 123417.

Genus LEVISOCERAS Foerste, 1925
LEVISOCERAS COMPLANATUM Ulrich, Foerste, & Miller
Plate 70, figures 17, 18

Levisoceras complanatum ULRICH, FOERSTE, & MILLER, 1943, Geol. Soc. America, Special Paper 49, p. 135, pl. 63, figs. 14–18.

This species, which is rather distinctive, is represented by only one specimen in the collection being studied. This specimen is a chert internal mold of most of the living chamber and a small portion of the siphuncle. The living chamber is about 25 mm. long and 18 mm. wide. It is broadly oval in cross section with the dorsum being very slightly narrower than the venter. It is curved endogastrically.

The septa are deeply concave and their impressions on the mold of the siphuncle indicate that they were very closely spaced. The sutures are sinuous with broad shallow lateral lobes and a rather high dorsal saddle. The ventral portion of the specimen is concealed in matrix but it seems most likely that the suture here formed a low saddle.

The apertural margin appears to have been oblique and to have formed a strong dorsal salient. Traces of growth lines on the living chamber are parallel with the apertural margins and essentially parallel with the suture.

The siphuncle is large, being 9.5 mm. wide at its adoral end. It is elliptical in cross section and is ventral in position.

Remarks.—This specimen is somewhat larger and more nearly round than the holotype, but its general physiognomy and the large size of the siphuncle seem to indicate that it is conspecific.

Occurrence.—Tanyard formation, Threadgill member. USGS TF-44.

Repository.—USNM 123418.

LEVISOCERAS ELLIPTICUM Ulrich, Foerste, & Miller
Plate 70, figures 3–7

Levisoceras ellipticum, ULRICH, FOERSTE, & MILLER, 1943, Geol. Soc. America, Special Paper 49, p. 138, pl. 63, figs. 7–13.

When this species was first described one specimen was stated to have come from a Gasconade horizon at some unrecorded locality in central Texas. There are now available four specimens from recorded localities which also belong to this species. Two of these are chert internal molds of living chambers, one is a mold of a small segment of a phragmacone, and the fourth is a mold of a living chamber attached to a piece of matrix in which is embedded part of the phragmacone.

The two specimens representing living chambers are almost identical, but one is slightly more complete. It is 11.5 mm. long, elliptical in cross section, and gradually expanded orad. The dorsal margin is slightly convex and the ventral slightly concave, indicating an endogastric curvature. Near the mid-length the living chamber is 8.6 mm. wide and 9.8 mm. high.

The siphuncle is very small, being only 0.9 mm. in diameter at the adapical end of the living chamber.

The phragmacone specimen shows that the camerae are less than 1 mm. in length, and that the sutures are essentially straight and slightly oblique; sloping orad from the venter to the dorsum. These characteristics are also shown by the fourth specimen.

Remarks.—This species is very similar in appearance to *Dakeoceras* sp. illustrated by Ulrich, Foerste, and Miller (Pl. 56, figs. 8, 9) but is slightly more rapidly expanded and has a much smaller siphuncle.

Occurrence.—The described specimen, and the phragmacone fragment are from the upper 75 feet of the Tanyard formation, Staendebach member, UM loc. 1. The other specimens are from the Tanyard formation, Staendebach member, USGS loc. 28.

Repository.—UM 11745A, 11745B, and USNM 123419, 123420.

LEVISOCERAS OBLIQUATUM Ulrich, Foerste, & Miller
Plate 70, figures 8, 9

Levisoceras obliquatum ULRICH, FOERSTE, & MILLER, 1943, Geol. Soc. America, Special Paper 49, p. 139, pl. 64, figs. 14–18.

The strongly oblique sutures on two small chert internal molds suggest that these specimens belong in this species.

The larger of the two is a strongly curved portion of a phragmacone approximately 9 mm. long on the ventral side and 21 mm. long on the dorsal side. Near the mid-length the conch is about 12 mm. high.

The camerae are very short, averaging about 1 mm. The septa curve strongly orad from the venter and are oblique to the long axis. The sutures are nearly straight along the ventral and lateral zones but form fairly high saddles over the dorsum. The siphuncle is large, being approximately half as high as the conch. It is oval in cross section, being compressed laterally.

The smaller specimen exhibits the same oblique sutures and short camerae as other members of the species and despite its incompleteness its specific identity is not much in doubt.

Remarks.—The siphuncle in the larger of the two specimens is somewhat larger than in the holotype of the species, but not sufficiently so to justify erection of a new species.

Occurrence.—The larger specimen is from the Staendebach member of the Tanyard formation, USGS loc. TF-397 and the smaller one from the same member, TB loc. 16T-2-59A.

Repository.—Small specimen, TB 32516, large specimen USNM 123421.

LEVISOCERAS PERCURVATUM Ulrich Foerste, & Miller
Plate 70, figure 16

Levisoceras percurvatum ULRICH, FOERSTE, & MILLER, 1943, Geol. Soc. America, Special Paper 49, p. 140, pl. 65, figs. 13, 14.
Levisoceras sp. CLOUD & BARNES, 1948 [1946], Univ. Texas Publication 4621, pl. 39, fig. 23.

The specimen being referrred to this species is a strongly curved endogastric brevicone consisting almost entirely of a chert mold of the phragmacone. The length, measured along the curved surface of the dorsum, is about 40 mm. of which only about 5 mm. at the adoral end may be a

mold of part of the living chamber. At the adapical end of the specimen the phragmacone is 8 mm. high and 6 mm. wide. The cross section is oval with the dorsum being more narrowly rounded than the venter. The camerae are about 1 mm. in length. The septa are mildly concave and are not strongly curved. The sutures are only slightly sinuous forming shallow lateral lobes and moderately high dorsal saddles. The ventral portion of the suture is not preserved. The sutures are nearly transverse to the long axis of the shell but slope orad along the dorso-lateral zones.

The siphuncle is moderately large and is oval in cross section. It is ventral in position.

Remarks.—This specimen is very similar to *L. obliquatum* but is larger and the sutures are less strongly oblique.

Occurrence.—Middle third of the Threadgill member of the Tanyard formation, USGS loc. TF-41A.

Repository.—USNM 123432.

LEVISOCERAS MAGNUM Unklesbay, n. sp.
Plate 70, figures 14, 15

Levisoceras ellipticum ? ULRICH, FOERSTE, & MILLER, 1943, Geol. Soc. America, Special Paper 49, p. 138, pl. 63, figs. 5, 6.

In 1943 Ulrich, Foerste, and Miller published two illustrations of a specimen which they questionably referred to *L. ellipticum*, and stated that, ". . . the specimen represented by Figures 5 and 6 on this plate [Plate 63] may not be at all closely related." In the Texas collection being presently studied there is a poorly preserved specimen which seems to be conspecific with the illustrated one. Consequently a new species is being established with their specimen, U.S.N.M. No. 108424, as the holotype.

The Texas specimen is an internal mold of the phragmacone about 42 mm. long. At the adapical end the cross section is elliptical and the mold is 12 mm. wide and 14 mm. high. It expands orad gradually and although the preservation is not good it seems to have been about 20 mm. wide at the adoral end.

The sutures are oblique to the long axis, but not as strongly so as in *L. obliquatum* or *L. percurvatum*.

The siphuncle is moderately large and is elliptical in cross section. At the adapical end of the specimen it is about 3 mm. in diameter. Its structure cannot be readily determined.

Remarks.—This species is larger than most of the species of this genus, hence the specific name *L. magnum*.

Occurrence.—The holotype is from the Oneota formation of Vernon County, Wisconsin. The Texas specimen is from the Tanyard formation, Staendebach member, USGS loc. 30.

Repository.—Holotype, USNM 108424; hypotype, USNM 123423.

Family PROTOCYCLOCERATIDAE Kobayashi
Genus WALCOTTOCERAS Ulrich & Foerste, 1936
WALCOTTOCERAS OBLIQUUM Ulrich, Foerste, Miller, & Unklesbay
Plate 71, figures 1–4

Walcottoceras shannonense [nomen nudum] ULRICH, 1928, Missouri Bur. Geology Mines, 2d. ser., vol. 22, p. 68.

Walcottoceras shannonense [nomen nudum] ULRICH, 1930, Missouri Bur. Geology Mines, 2d. ser., vol. 23, p. 159.

Walcottoceras shannonense [nomen nudum] POWELL, 1935, St. Paul., Inst., Sci. Mus., Sci. Bull. 1, pp. 35, 37, 67–68, pl. 7, figs. 1–5.

Walcottoceras shannonense [nomen nudum] STAUFFER & THIEL, 1941, Minn. Geol. Survey, Bull. 29, p. 246.

Walcottoceras obliquum ULRICH, FOERSTE, MILLER, & UNKLESBAY, 1944, Geol. Soc. America, Special Paper 58, pp. 89–90, pl. 45, figs. 3–19; pl. 46, figs. 3–11.

Ectenoceras spp. CLOUD & BARNES, 1948 [1946], Univ. Texas Publ. 4621, pl. 39, figs. 20, 21, 22.

Four excellent specimens and several fragments are available for study. The most nearly complete of the four is about 46 mm. long and about 27 mm. of this length is phragmacone. It is slightly curved endogastrically and gradually expands from 6 mm. in height at the adapical end to 10 mm. at the adoral end. The cross section is broadly elliptical. Throughout the length of the specimen there are strong rounded annulations. On the phragmacone they are directly transverse and nearly parallel with the sutures but on the living chamber they are oblique, sloping orad from the venter.

The sutures are sinuous, very slightly oblique, and form dorsal and ventral saddles and broad lateral lobes. The dorsal saddle

rises higher than the ventral.

One large specimen seems to represent nearly all of a living chamber about 45 mm. long. It is orthoceraconic and expands orad very slightly from a height of 15 mm. at the adapical end to 17 mm. at the aperture. This chert mold is strongly annulated with the annulations crossing the long axis of the shell at an angle of about 78 degrees, and sloping orad from the venter to the dorsum. Both the crests and troughs of the annulations are striated. The cross section is ovate with the venter being slighly more narrowly rounded than the dorsum. The aperture is essentially unmodified and the margin forms shallow lateral lobes and low ventral and dorsal saddles. This specimen is larger than others of this species but does not appear specifically distinct.

Another specimen is a chert internal mold of a considerable portion of a phragmacone. It is 31 mm. long and at mid-length is 11 mm. high. This specimen is strongly annulated with the annulations being oblique to the long axis and diagonally transverse to the sutures. The camerae are short, about 1 mm. in length, and the sutures slope slightly apicad as they cross from the venter to the dorsum. The siphuncle is small, and ventral in position. It is also marked by strong oblique annulations.

The smallest specimen is very similar to the one just described, but consists of a mold of the adapical portion of a strongly annulated living chamber. There is a small portion of the siphuncle attached. It is only about 2 mm. in diameter where the height of the conch is 7 mm.

Remarks.—There are also available several fragmentary specimens which may belong to this species. None of them is septate, however, and they cannot be certainly differentiated from the fillings of cyrtochoanitic siphuncles of some other genus. The specimens illustrated by Cloud and Barnes on Plate 39 appear to be conspecific.

Occurrence.—Two of the illustrated specimens are from the Tanyard formation, Staendebach member, USGS loc. 28. The third is from the same member at USGS loc. TF-37. The largest specimen described is from a Gasconade horizon 3¼ miles north of Point Peak, Llano County Texas.

Repository.—USNM 123424–123427.

Walcottoceras helleri
Unklesbay, n. sp.
Plate 71, figures 5–7

Two fragmentary chert internal molds form the basis for this species and the better of the two is chosen as the holotype. It is about 35 mm. long and consists almost entirely of phragmacone; the adoral 3 mm. seems to be the base of the living chamber. The conch is long, straight, and expands very slightly orad. It is about 6 mm. in dia-

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Explanation of Plate 70

Figs. *1, 2*—*Dakeoceras* cf. *D. perretrorsum* Ulrich, Foerste, and Miller, lateral views, ×1½, of two specimens from the Staendebach member, TB loc. 16T-2-59A, TB 32497 (fig. 1), 32496 (fig. 2). (p. 638)

3–7—*Levisoceras ellipticum* Ulrich, Foerste and Miller, ventral and lateral views of one specimen, UM 11745A, and lateral views of another, UM 11745B, both from Staendebach member of UM loc. 1; and lateral and dorsal views of specimens from same member at USGS loc. 28, USNM 123419 (fig. 6), 123420 (fig. 7). All views ×2. (p. 650)

8, 9—*Levisoceras obliquatum* Ulrich, Foerste, and Miller, lateral views, ×2, of specimen from Staendebach member, USGS loc. TF-397, USNM 123421; and lateral view, ×2, of fragment from Staendebach member, TB loc. 16T-2-59A. TB 32516. (p. 650)

10—*Dakeoceras* cf. *D. normale* Ulrich, Foerste, and Miller, lateral view, ×1½, of small specimen from Staendebach member USGS loc. 28, USNM 123403. (p. 638)

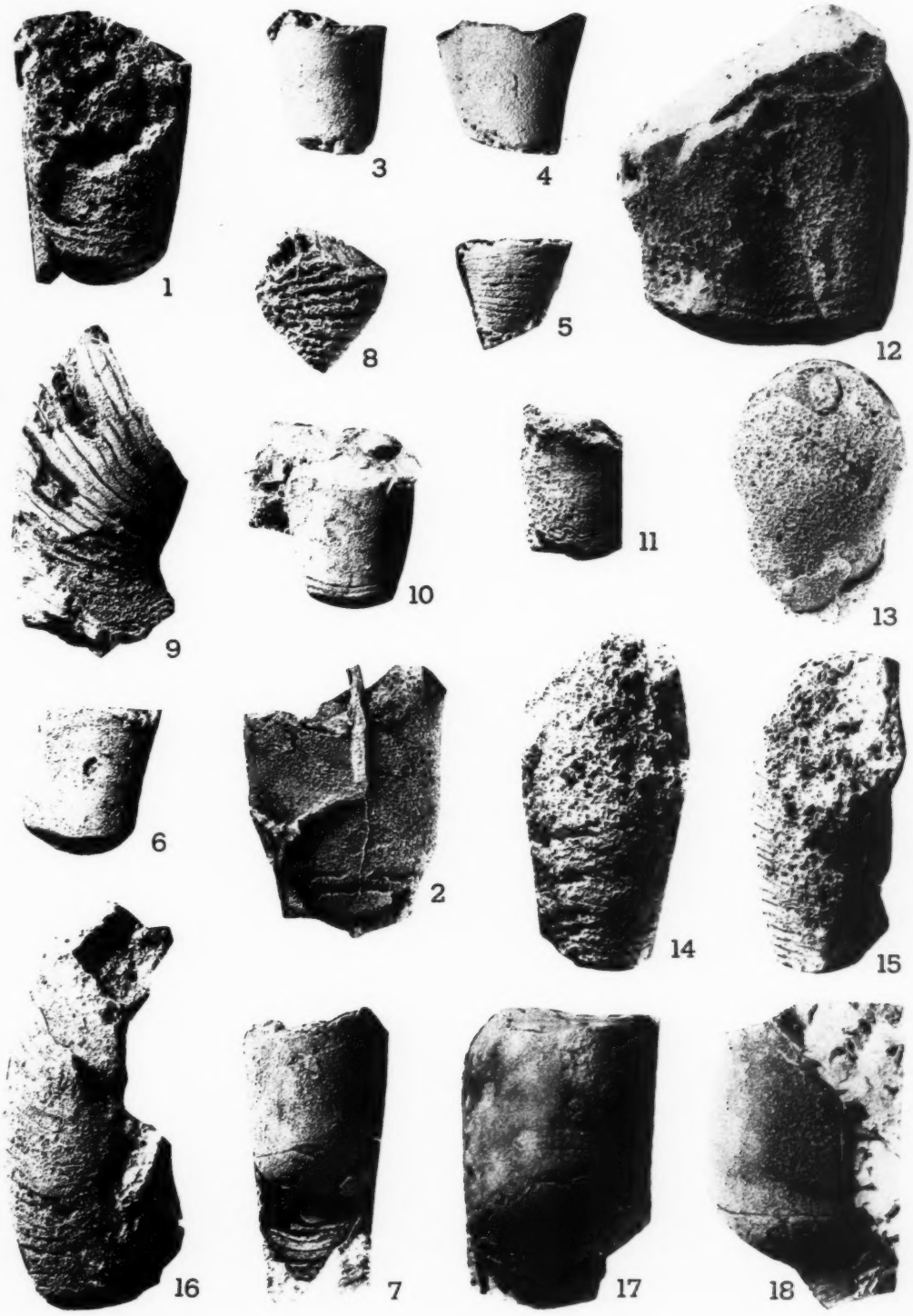
11—*Ectenoceras laqueatum* Ulrich, Foerste, and Miller, lateral view, ×1, of specimen from Staendebach member at USGS loc. 30, USNM 123413. (p. 648)

12, 13—*Oneotoceras loculosum* (Hall), lateral and septal views, ×2, of specimen from Staendebach member, TB loc. 149T-7-15A, TB 32515. (p. 647)

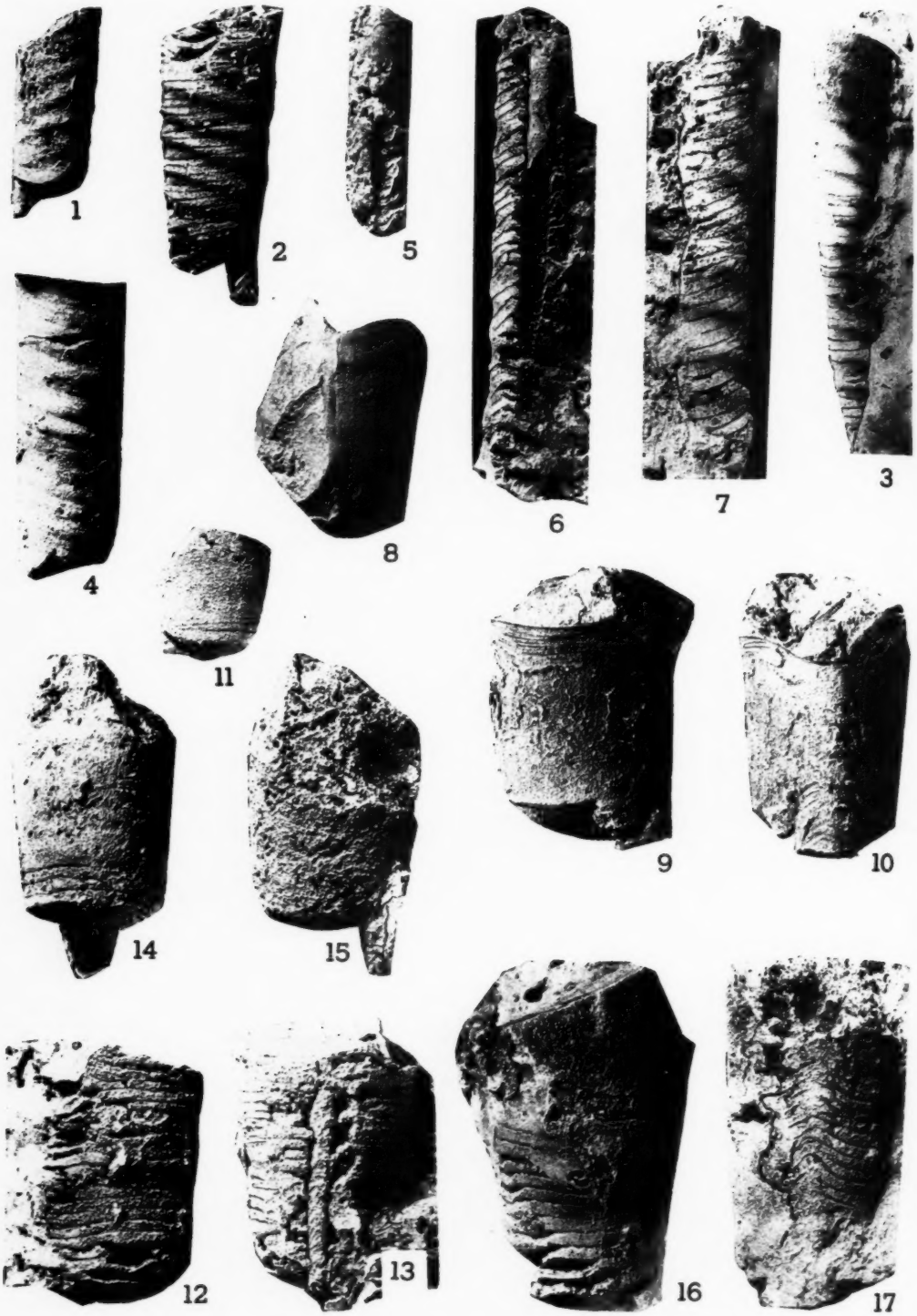
14, 15—*Levisoceras magnum* Unklesbay, n. sp., dorsal and lateral views, ×1, of a specimen from the Staendebach member at USGS loc. 30, USNM 123423. (p. 651)

16—*Levisoceras percurvatum* Ulrich, Foerste, and Miller, lateral view, ×1½, of specimen from the Threadgill member USGS loc. TF-41A, USNM 123422. (p. 650)

17, 18—*Levisoceras complanatum* Ulrich, Foerste, and Miller, dorsal and lateral views, ×1½, of specimen from the Tanyard formation at USGS loc. TF-44, USNM 123418. (p. 649)



Unklesbay, Ordovician (Tanyard) nautiloids, Texas



Unklesbay, Ordovician (Tanyard) nautiloids, Texas

meter and circular or nearly so in cross section.

The camerae are very short, averaging only about 0.8 mm. in length. The sutures are slightly sinuous, forming broad shallow lateral lobes, a very low dorsal saddle and a higher ventral saddle. The siphuncle is relatively large, approximately 2 mm. in diameter, and is ventral in position.

This internal mold bears strong rounded annulations which slope orad from the venter and are oblique to the sutures. In crossing from the venter to the dorsum each annulation extends across five or six camerae

The paratype is slightly smaller in diameter. It is 18 mm. long, of which 7 mm. is living chamber.

Remarks.—This species differs from other species of *Walcottoceras* in the strong obliquity of the annulations, and in the marginal position of the siphuncle. The specific name is for Robert Leo Heller who collected the specimens.

Occurrence.—Upper 75 feet of the Tanyard formation, Staendebach member, UM loc. 1.

Repository.—UM 11748 (holotype) 11747 (paratype).

DESCRIPTIONS OF LOCALITIES

University of Missouri (UM)

Loc. 1—San Saba Co. About one third of the way up a south-facing slope overlooking Rough Creek, just northeast of Rough Creek Spring, about 9.7 miles, by speedometer, southeast of San Saba on road to Chappel. Coll: R. L. Heller, Nov. 1949.

U. S. Geological Survey (USGS)

Loc. 28—San Saba Co. Barnes Ranch. On top of a small 1500′ knob crossed by secondary road east of Long Waterhole Branch and north of Marley Creek. Extreme northeast corner of Llano quad. Main collecting ground about 100′ east of road. J. Bridge, 10/20/34.

Loc. 30—Llano Co. in hollow about 1 mile southwest of BM 1559, and 0.6 mi. north of first gate on road to Everett Ranch, east side of road. J. Bridge, 10/8/34.

Loc. 57—San Saba Co., chert in road ditch near summit of knob, about 9–9.1 miles north of cross-roads at Cherokee, on Llano-San Saba highway. J. Bridge. 5/20/31.

Loc. B-36—San Saba Co. 1500 to 2500 feet south of bridge abutment at crossing of Texas Hwy. 16 over Buffalo Creek. Fossils in chert. Threadgill member, Tanyard formation. Coll: P. E. Cloud Jr. 12/17/43.

Loc. B-52—San Saba Co. From entrance to Perry Ranch house to about 400 feet south of there in open field on east side of Texas Hwy. 16. Fossils in limestone and chert. L. Ordovician—Gasconade. Coll: R. L. Heller, P. E. Cloud Jr. 12/17/43.

Loc. TF-37—San Saba Co. Approximately 7.3 miles south of San Saba and 1.6 miles east of Hwy. 16, due east of a point 0.1 mile north of entrance to Flying V Ranch. About 1.8 miles airline S. 40°W. from

EXPLANATION OF PLATE 71

FIGS. *1–4*—*Walcottoceras obliquum* Ulrich, Foerste, Miller, and Unklesbay, lateral view, ×1½, of specimen from Staendebach member, USGS loc. 28, USNM 123424; lateral view, ×1½, of specimen from same member, USGS loc. TF-37, USNM 123425; lateral view, ×1½, of specimen from same locality as fig. 1, USNM 123426; and lateral view of large specimen from a Gasconade horizon 3¼ miles north of Point Peak, Llano County, Texas, USNM 123427. (p. 651)

5–7—*Walcottoceras helleri* Unklesbay, n. sp., ventral view of small paratype, and ventral and lateral views of holotype, all ×2, from Staendebach member, UM loc. 1, UM 11747 paratype, and 11748 holotype. (p. 652)

8—*Buehleroceras apertum* Ulrich, Foerste, and Miller, ventral view, ×1½, of specimen from Staendebach member, USGS loc. 28, USNM 123412. (p. 647)

9, 10—*Eremoceras sansabaense* Unklesbay, n. sp., lateral and ventral views of holotype, ×1½, from upper Gasconade at USGS loc. TF-37, USNM 123417. (p. 649)

11–13—*Eremoceras subrectum* Ulrich, Foerste, and Miller, lateral view, ×1½, of small specimen from Staendebach member, UM loc. 1, UM 11746; and lateral and ventral views, ×1½, of a specimen from the same member, TB loc. 27T-7-56A, TB 32517. (p. 648)

14–17—*Eremoceras teres* Ulrich, Foerste, and Miller, dorsal and lateral views, ×1½, of specimen from Threadgill member, USGS loc. TF-41, USNM 123416; and lateral and ventral views of specimen from a Gasconade horizon at USGS loc. B-36, USNM 123415. (p. 648)

W. R. Payne ranch house, from 500 to 800 feet east of the north-south fence line bounding Perry's ranch on the west and 2300 to 2600 feet north of the east-west fence line at the south of Perry's ranch. On a flat at the top of the divide between drainage through Buffalo Creek to the south and through Elm and Simpson Creeks to the north, in clearing among live oaks. Fossils in chert weathered from dolomite and limestone. L. Ordovician—upper Gasconade. [Staendebach] Coll: P. E. Cloud, Jr., R. L. Heller, 1/4/44.

Loc. TF-41—San Saba Co. About 2¼ miles north of Cherokee and 3000 feet west of Texas Hwy 16. Near top of northeast-southwest trending hill at head of large open draw. Fossils in chert. L. Ordovician—lower Gasconade. [Threadgill] Coll: R. L. Heller, 1/6/44.

Loc. TF41-a—San Saba Co. About 900 feet south of TF-41 at foot of south slope of hill. Fossils in chert. L. Ordovician, lower Gasconade. [Threadgill—Tanyard] Coll: P. E. Cloud, Jr., 1/11/44.

Loc. TF-44—San Saba Co. About 4.5 miles by speedometer north-northeast of Cherokee and 750 feet due east of a point 700 feet south-southwest on unfenced county road from point where private road to J. E. Epperson ranch house takes off to north just south of big bend in Cherokee Creek. On the gentle west slope of a hill between two small draws. Fossils in chert. L. Ordovician—lower Gasconade. [Threadgill] Coll: R. L. Heller, 1/8/44.

Loc. TF-51—San Saba Co. About 4.5 miles north of Cherokee. From 2000 to 2300 feet east a little north along a fence line going east from Texas Hwy. 16 from a point a little over a mile by speedometer south of its crossing over Buffalo Creek. From 100 to 300 feet north of fence line on northeast slope of hill near peak, between fence and road to Bill Porch's ranch. Fossils in chert. Lower Ordovician—lower Gasconade. [Threadgill] Coll: P. E. Cloud Jr., R. L. Heller 1/11/44.

Loc. TF-63—San Saba Co. From a point 5.1 miles by speedometer north-northeast of Cherokee (1100 feet east of the 7th cattle guard) on the road to Rough Creek Spring the locality is about 1600 feet due south. Fossils in chert float among sparsely scattered cedars about one-third of the way up a scarp slope from just below the head of a wash. Lower Ordovician—lower upper or upper middle Gasconade. Coll: P. E. Cloud, Jr., 2/10/44.

Loc. TF-110—San Saba Co. Approximately 5.6 miles airline south-southeast of San Saba. One mile along the Rough Creek Spring road from its juncture with the Chappel-San Saba road and then 4700 feet due west. On southwest facing slope about 250 feet north of break on slope and a gravel road leading into windmill and tank of the Epperson Ranch. Fossils in chert. Lower Ordovician—upper Gasconade. [Tanyard–Staendebach] Coll: R. L. Heller, 4/17/44.

Loc. TF-130—San Saba Co. Cherokee area. Approximately 6.59 miles airline S. 7°W. from the intersection of Highways U. S. 90 and Texas 16, at San Saba. About 7.9 miles by speedometer south from San Saba along Texas Hwy. 16 and thence 330 feet due east. At the southeast corner of a cleared fenced field on the H. C. Perry ranch. Fossils in loose blocks of chert piled around fence post. Lower Ordovician—Tanyard formation Staendebach member.

Loc. TF-371—Llano Co. Moore Hollow section. From chert float between 540 and 580 feet in the Moore Hollow section, probably derived principally from 550 to 580 feet and above. Lower Ordovician, Tanyard formation (float over upper beds of Threadgill member, probably derived in part if not entirely from lower beds of Staendebach member above).

Loc. TF-397—McCulloch Co. About 2400 feet south of High Lonesome Mill, Tanyard formation, Staendebach member.

Loc. TF-404—McCulloch Co. Bald Ridge area. About 850 feet due east from TF-402 at the top of a small knoll on west side of a gentle south-trending spur. Fossils in chert. Lower Ordovician, Tanyard formation, Staendebach member (about 25 feet below top).

Texas Bureau of Economic Geology (TB)

Loc. 16T-2-59A—Blanco County—Johnson City area—1¼ miles airline NE of Johnson City on north bank of Pedernales River. 500 feet downstream (east) of

Highway bridge. Fossils in chert float along fence; 38 feet below top of Staendebach member of the Tanyard formation. Collected by V. E. Barnes and L. E. Warren in 1944.

Loc 16T-6-15A—Blanco County-Johnson City area—2 miles airline WNW of Johnson City, 1¼ miles by road N of Fredericksburg Highway, 300 feet NW of road crossing of Towhead Creek. Fossils in chert in E road ditch in part as float and in part in dolomite. Estimated to be about 38 feet below the top of the Staendebach member of the Tanyard formation. Collected by V. E. Barnes and L. E. Warren in 1942.

Loc. 27T-5-55A—Burnet County-Post Mountain area—2200 feet southwest of Burnet County Court House under power line 1300 feet WNW of bridge over Hamilton Creek, 1500 feet NW from point where power line crosses Marble Falls highway. Chert fossils in dolomite. Dolomitic facies of the Threadgill member of the Tanyard formation. Collected by V. E. Barnes and L. E. Warren, 1944.

Loc. 27T-5-55B—400 feet WNW of locality 27T-5-55A, 75 feet NE of fence corner. Chert fossils in dolomite. Dolomitic facies of the Threadgill member of the Tanyard formation. Collected by V. E. Barnes and L. E. Warren, 1944.

Loc. 27T-7-42A—Burnet County—Tanyard area—5 miles airline NE of the Tanyard, about 3 miles W of the Naruna-Nix road, about ¾ mile east of the Vann Camp-Tanyard road intersection and along the Tanyard road to the SE end of a field about ¼ mile east of a ranch house. Chert fossils in float. Near top of Staendebach member of Tanyard formation. Collected by V. E. Barnes.

Loc. 27T-7-56A—Burnet County—Tanyard area—4200 feet ENE of Tanyard Spring 1800 feet NE of cattleguard, 100 feet NW of road and just north of power line. Chert fossils in float. Upper part of Staendebach member of Tanyard formation, calcitic facies. Collected by V. E. Barnes and L. E. Warren, 1944.

Loc. 27T-9-4A—Burnet County—Sudduth area—2 miles airline N of Sudduth, 2400 feet ENE of Highway bridge over Honey Creek, 3500 feet NNW from junction of Honey and Hamilton Creeks, 700 feet W of Hamilton Creek. Chert fossils in float. Staendebach member (?) of Tanyard formation, dolomitic facies. Collected by V. E. Barnes and L. E. Warren, 1943.

Loc. 27T-9-6A—Burnet County—Sudduth area—1700 feet ESE of Sudduth, along western edge of a depression 400 feet in diameter. Chert fossils in float. Dolomitic facies of the Threadgill member of the Tanyard formation. Collected by V. E. Barnes and L. E. Warren, 1943.

Loc. 27T-9-6C—Burnet County—Sudduth area—3000 feet south of Sudduth, 1700 feet SSE of railroad crossing, 900 feet E of the south edge of a roadside park. Chert fossils in float. Dolomitic facies of the Threadgill member of the Tanyard formation. Collected by V. E. Barnes and L. E. Warren, 1944.

Loc. 27T-9-25C—Burnet County—Backbone Ridge—1¼ miles SE of Longhorn Cavern, 100 feet N of old road leading SE from Longhorn Cavern about ½ mile from park boundary fence. Chert fossils in float. Dolomitic facies of the Staendebach member of the Tanyard formation. Collected by V. E. Barnes and L. E. Warren, 1944.

Loc. 27T-9-46A—Burnet County—Backbone Ridge area—2 miles airline ESE of Kingsland, 4500 feet N of railroad and ballast pit, 3200 feet SE of power line, 2000 feet E of a fence corner, 1000 feet S of a fence corner. Chert fossils in float. Estimated to be 45 feet above base of dolomitic facies of the Threadgill member of the Tanyard formation. Collected by V. E. Barnes and L. E. Warren, 1943.

Loc. 27T-9-46B—Burnet County—Backbone Ridge area—600 feet E of locality 27T-9-46A. Probably float from west of a fault and from the dolomitic facies of the Threadgill member of the Tanyard formation. Collected by L. E. Warren, 1944.

Loc. 27T-9-46D—Burnet County—Backbone Ridge area—2¼ miles airline E of Kingsland, 100 feet S of Mill Creek, at a point where fence crosses creek 2300 feet ESE of power line, 500 feet ESE of fence. Chert fossils in float. Near top of Staendebach member of Tanyard formation. Collected by L. E. Warren, 1944.

Loc. 149T-7-15A—Llano County—Lone

Oak Mountain area—3½ miles ENE of the town of Field Creek and on Lone Oak Mountain ½ mile west of Bee triangulation Station and about ½ mile east of Cold Creek, 1150 feet N of a fence and 1900 feet NW of a fence corner. Probably high Staendebach of the Tanyard formation. Collected by V. E. Barnes and L. E. Warren, 1944.

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JURASSIC STROMATOPOROIDS FROM THE LEBANON

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ABSTRACT—Stromatoporoids from the Upper Jurassic of the Lebanon are named and described as *Actinostromaria* sp. cf. *Actinostroma praesalevensis* Zuffardi-Comerci, *Cladocoropsis dubertreti* Hudson, *Milleporidium libanoticum* n. sp., *Parastromatopora libani* n. sp., *Stromatoporina* cf. *S. douvillei* (Dehorne) and *Syringostromina* sp. The subgenus *Parastromatopora* Yabe and Sugiyama is raised to generic rank.

INTRODUCTION

THE SMALL group of Jurassic stromatoporoids described in this paper were collected by F. Heybroek in 1937–38 during field-work in the southern Lebanon (Heybroek, 1942). Permission to describe these specimens was readily given to the author by Dr. Heybroek and by the authorities of the Rijksmuseum van geologie en mineralogie te Leiden, where the collection is now housed. A small but representative sample of the specimens was presented by the Rijksmuseum to the British Museum (Natural History); these are referred to in this paper by an index number preceded by the letter H. The author is indebted to the Chief Geologist and the Directors of the Iraq Petroleum Company Limited for permission to publish this work carried out under their aegis.

THE MATERIAL: ITS LOCALITY AND HORIZON

The area of the southern Lebanon mapped by Dr. Heybroek is centred on Djebel Barouk, and includes the southern part of the plain of Bekaa to the east and part of the plateau area to the west. The localities from which the fossils were collected, and all place names mentioned in this paper, can be found in the maps and sections of the paper by Dr. Heybroek (1942) in which he so ably describes the geology of the area.

The upper part of the Jurassic succession of the area is as follows (the thicknesses are those of the succession at Toumatt Djezzine, see Heybroek, 1942, fig. 17 and p. 319):

Portlandian

Couches jaunes supérieures (shelly marly limestone)	15 m.
Falaise de Djisr el Qadi (compact grey-brown limestone with chert)	55 m.
Couches jaunes inférieures (bedded limestone, mostly marly)	75 m.

Kimmeridgian-Sequanian

Calcaires à *Cidaris glandaria* (light-grey compact limestone)	50 m.±

The upper part of the *glandaria*-limestones contains a shallow water fauna in which Heybroek (1942, p. 323) records, as abundant, the stromatoporoids *Burgundia ramosa* Pfender, *Stromatopora douvillei* Dehorne, and *Lovcenipora vinassai* Giattini. Specimens of the last from these beds in Djebel Barouk (Localities FL106, FL140, FL144, FL149) form the main part of the collection sent to the author (numbers preceded by the letters FL are the locality index field-numbers of Dr. Heybroek. Details of the localities are given later). South of the Djebel Barouk range, Jurassic limestones are exposed on the eastern slopes of Toumatt Djezzine (Heybroek, 1942, fig. 318 and p. 319) and from there (Localities FL177 and FL211), apparently from a slightly lower level than the *Lovcenipora* limestones, specimens of *Actinostromaria* and *Milleporidium* were collected. Heybroek (1942, p. 322) also records the occurrence of stromatoporoids in the limestone of the Falaise de Djisr el Qadi and his collection includes a specimen of "*Stromatoporina*" from these beds (FL251) in the Abeih area (Heybroek, 1942, p. 298). The remaining specimens (FL209 A, B) are species of *Parastromatopora* and *Syrigostromina* from the Couches jaunes inf. of T. Djezzine.

Age.—The *glandaria*-limestones and the included *Lovcenipora* limestones are considered by G. Heybroek (1942) to be of Kimmeridgian age. Other sections of these beds in the Lebanon have recently been studied by Renouard (1951) who considers the *glandaria*-limestones to be upper Lusitanian (Rauracian-Sequanian) and the immediately overlying strata to be Kimmeridgian. This age allocation, rather than that of Heybroek, is adopted by the author since it agrees with the age of comparable stromatoporoid faunas occurring elsewhere in the Middle East.

SYSTEMATIC PALAEONTOLOGY

Genus ACTINOSTROMARIA Dehorne, 1917

ACTINOSTROMARIA sp. cf. ACTINOSTROMA PRAESALEVENSIS Zuffardi-Comerci

Plate 72, figures 1, 2

The specimen (piece 3 and thin sections 3A, 3B) named as above was collected from the eastern slopes of Toumatt Djezzine, 2.9 km. N. 82° E. of Toumatt (Locality FL177, Heybroek, 1942, fig. 17, p. 318). It is part of a well-preserved nodular coenosteum, about 2 cm. across, of *Actinostromaria*. The pattern of its reticulum is similar to that of *Actinostroma praesalevensis* Zuffardi-Comerci, 1932, except that both vertical pillars and concentric lamellae, and the resulting meshwork, are much finer, the pillars and their connecting lamellae being from 0.01 mm. to 0.025 mm. thick (0.02 common), the distance apart of such lamellae being about 0.15 mm. (compare 0.4 mm. of *A. praesalevensis*). In transverse section the vertical structures are seen to be both isolated pillars, and those connected to form meandriform lamellae: tubule formation is negligible (cf. *Actinostroma praesalevensis* Zuff.-Com., 1932, fig. 6b). In vertical section both pillars and concentric lamellae are seen to be discontinuous, the lamellae rarely extending across more than three or four pillars, the pillars themselves being much longer than the lamellae: the resulting pattern is markedly reticulate (cf. *A. praesalevensis* Zuff.-Com., Wells, 1943, pl. 9, fig. 7). Astrorhizal tubes are rare. The allocation of the species, probably an undescribed one, to *Actinostromaria* follows on the redefinition of that genus by Lecompte (1952).

Genus CLADOCOROPSIS Felix, 1907

CLADOCOROPSIS DUBERTRETI Hudson

The species of *Cladocoropsis* occurring in the upper part of the Calcaires à *Cidaris glandaria* and referred to by Heybroek, Dubertret and others as *Lovcenipora vinassai* Giattini or *Cladocoropsis mirabilis* Felix was redescribed in a recent paper by the author (1954) and named *Cladocoropsis dubertreti* Hudson. The species is well represented in the Heybroek collection by limestone pieces, each containing numerous branch fragments, from the following localities:—

FL106. Dj. en Nane, 2 km. S. 81° E. of Ain Zhalta. Specimen 1 and thin sections 1A, 1B.
FL140*. Dj. Barouk, 1.9 km. S. 41° E. of El Barouk. Specimens 1–3 (Specimen 3 is H4785, the holotype of *Cladocoropsis dubertreti*, see Hudson, 1954, Pl. 3, fig. 4).
FL144*. Dj. Barouk, 2 kms. N. 57° E. of Maaser ech Chouf. Specimens 1–3 (Specimen 3 is H4787).
FL149*. Same locality as FL144. Specimens 1-4 (Specimen 4 is H4786).

Localities marked * are indicated by an asterisk on the 1:50,000 map of the southern Lebanon by Heybroek (1942, pl. 9).

Genus MILLEPORIDIUM Steinmann, 1903

MILLEPORIDIUM LIBANOTICUM Hudson, n. sp.

Plate 72, figures 3–6;
Plate 73, figure 2

Several pieces of limestone (specimens 1-4 and thin sections 1A-1G) from Locality FL211*, Toumatt Djezzine, 2.9 km. S. 63° E. of Toumatt, include parts of one coenosteum of an undescribed *Milleporidium* which is here given specific identity as *M. libanoticum*, n. sp.

Holotype.—The above specimens and thin sections (Specimen 1 and thin sections 1A-1D are H4788).

Description.—Coenosteum of short proliferations (diam. from 5 mm. to 10 mm.; 7 mm. common) which frequently branch. The reticulum is composed of tabulate dimporphic tubules, the two sizes of tubules being definitely distinct, the diameter of the major ones being from 0.3 mm. to 0.6 mm. (0.4 mm. common) and that of the minor ones being from 0.07 mm. to 0.18 mm. (0.1 mm. common). The former are failry evenly spaced in the mesh formed by the minor

ones, but have no independent wall, being formed as gaps in the tubule mesh and thus having an irregular outline in cross section: the minor tubules are usually rounded in cross section but may be elongate or irregularly polygonal. The tubule walls are from 0.05 mm. to 0.09 mm. thick, 0.07 being common. In the axial part of the branches the tubules are vertical, bending peripherally to become normal to the branch surface, and thus forming an axial and peripheral reticulum. The major tubules are initiated in the axial reticulum by the expansion of a minor tubule: they thus occur mainly in the peripheral reticulum, the axial reticulum tending to be monomorphic. The major tubules tend to be arranged in line and may link together, forming an irregular nontabulate tube within the reticulum but independent of its pattern: they may be the initial division between branches; they are not astrorhizal tubes.

There are no coenosteal lamellae or latilamellae in the reticulum. The tubule walls are microfibrous, the fibres extending upwards and outwards from a central plane of initial calcification (jet d'eau structure) which does not differ in colour from the fibres themselves.

Comparison.—Three species of *Milleporidium*, *M. remesi* (Steinmann, 1903) from the Tithonian of Stramberg, *M. steinmanni* (Yabe and Sugiyama, 1935) from the Upper Jurassic of Japan, and *M. somaliense* (Zuffardi-Comerci, 1932, 1938) from the Upper Jurassic of Somaliland, are similar to *M. libanoticum* in that they have a markedly dimorphic peripheral reticulum. The last two of these are columnar and branching as *M. libanoticum* but differ from that species since, in each, the peripheral reticulum tends to be laminar, due in *M. remesi* to latilamellae and in *M. somaliense* to pseudolatilamellae. *M. steinmanni* is massive and so differs from the columnar *M. libanoticum*.

Genus PARASTROMATOPORA Yabe and Sugiyama, 1935

PARASTROMATOPORA LIBANI Hudson, n. sp.

Plate 73, figures 1, 3, 4

The one specimen, about 10 cm. in diameter, of this species was collected by Dr. Heybroek from the Couches jaunes inférieures (Upper Jurassic) of Toumatt Djezzine, 2.7 km. S. 66° E. of Toumatt (Locality FL209, Heybroek, 1942, p. 318, fig. 17).

Holotype.—The above specimen, which now consists of five pieces (1–5) and four thin sections (1A, 1B, 2A, 4A). Pieces 1, 4, and thin sections 1A, 1B are registered as H4789 in the collections of the Geological Department, British Museum (Natural History); the remainder are in the collections of the Rijksmuseum van geologie te Leiden.

Description.—The coenosteum, partly silicified, is massive, nodular, and internally laminar. The better preserved parts of the surface show a mesh formed by the ostia of the coenosteal tubules and an occasional stellate astrorhizal system. The reticulum is formed by fairly continuous radial pillars linked by pillar lamellae and showing, in cross section, a monomorphic vermiculate mesh, the interspaces being crossed by abundant tabulae. Coenosteal lamellae do occur but do not, in general, interrupt the continuity of the radial pillars, the laminar character of the reticulum being due to variation in thickness of the skeletal elements. The pillar lamellae are from 0.12 mm. to 0.25 mm. thick, commonly 0.16 mm., the distance between them being commonly 0.2 mm. The tabulae are occasionally compound, the distance between them being commonly 0.26 mm. The astrorhizal tubes conform generally to the reticulum pattern though they are more continuous than the pillars, slightly wider than the interspaces, and more regularly tabulate. The structural elements, other than the tabulae, are microfibrous, the fibres being bunched upwards and outwards. Lines and centres of initial calcification were not seen.

Comparison.—*Parastromatopora libani* is similar in structural pattern to *Stromatopora choffati* Dehorne (Dehorne 1917, 1920) from the Lusitanian of Portugal (see Lecompte, 1952, p. 20). In this latter form, however, the pillars and pillar laminae are less dominant, the reticulum is strongly latilamellate and generally coarser, and the coenosteum discoidal. The reticulum pattern of *P. libani* is more like *"Stromatopora" subjaponica* Yabe and Sugiyama, 1935, and *Stromatopora torinosuensis* Yabe and Sugiyama, 1935, from the Upper Jurassic of

Japan, but in both these species the reticulum is coarser and its structural elements thicker than in *P. libani*. There is also considerable resemblance between the reticulum of *P. libani* and that of *Stromatopora kurtchensis* Wells, 1943, from the Upper Jurassic of Ethiopia, but this latter form has abundant astrorhizae and mamelons.

Generic allocation.—Lecompte (1952) has shown that the Mesozoic stromatoporoids formerly allocated to the genus *Stromatopora* differ from that genus by the microstructure of their skeletal elements, a difference, in the opinion of Lecompte so fundamental that it entails generic distinction. Most of the Mesozoic "*Stromatopora*" removed from that genus he placed in the genus *Stromatoporina* Kühn, 1927. The species *libani* cannot be so allocated since it lacks the coenosteal lamellation characteristic of *Stromatoporina*. It is, however, structurally similar and undoubtedly congeneric with *Stromatopora japonica* Yabe, 1903, the type of the subgenus *Parastromatopora* Yabe and Sugiyama, 1935. That subgenus is here, with the permission of Professor Yabe, raised to generic rank and the species *P. libani* is allocated to it.

Genus STROMATOPORINA Kühn, 1927
STROMATOPORINA cf. S. DOUVILLEI (Dehorne)

The one specimen of this species in the Heybroek collection is from locality FL251, gorge of Wadi Jerbane, 1.9 km. S. 62° E. of Kfer Matta (see Heybroek, 1942, fig. 7 and p. 298). The species is also recorded by Heybroek (1942, p. 448) from the *Lovcenipora* reef at Toumatt Djezzine.

The species founded by Dehorne (1918) on specimens from the Upper Jurassic of southern Tunisia was placed by her in the genus *Stromatopora*, and later by Lecompte (1952) in the genus *Stromatoporina* Kühn, 1927. Though the above specimen lacks the diagnostic lamellar reticulum of *Stromatoporina*, its preservation makes other generic allocation uncertain: it is, therefore, not reallocated.

Genus SYRINGOSTROMINA Lecompte, 1952
SYRINGOSTROMINA sp.

The specimen of the above form is from the same locality (FL209) and horizon as the specimen of *Parastromatopora libani* n. sp. described previously. It now consists of six pieces (B/1–6) and six thin sections (2A, 2B, 3A, 4A, 5A, 6A) all in the collections of the Rijksmuseum van geologie te Leiden. It is about 8 cm. in diameter, and is part of a nodule so silicified that none of the original surface remains. The reticulum is strongly laminated, the skeletal elements consisting of short pillars and their connecting pillar-lamellae, and continuous coenosteal lamellae not crossed by pillars. Such lamellae occur at irregular intervals and two or three may occur close together to form marked latilamellae. The reticulum pattern is a fine one, the pillar-lamellae being only 0.09–0.12 mm. thick, commonly 0.1 mm., and 0.08 mm. apart. Tabulae are rare in the interspaces. Astrorhizal tubes are common: they are long, vertical and strongly tabulate, the coenosteal lamellae being inclined upwards at their contact with them.

The allocation of this form to the genus *Syringostromina* Lecompte, 1952, is in doubt since the internal structure of the specimen on which it is based has been partly destroyed by silicification. Its reticulum pattern resembles that of *Syringostromina prvosti* Lecompte, 1952, the holotype of which came from the Lusitanian of Portugal, and which is the type species of the genus. Both forms have a nodular coenosteum with a fine reticulum consisting of closely spaced pillars and, at intervals, continuous coenosteal

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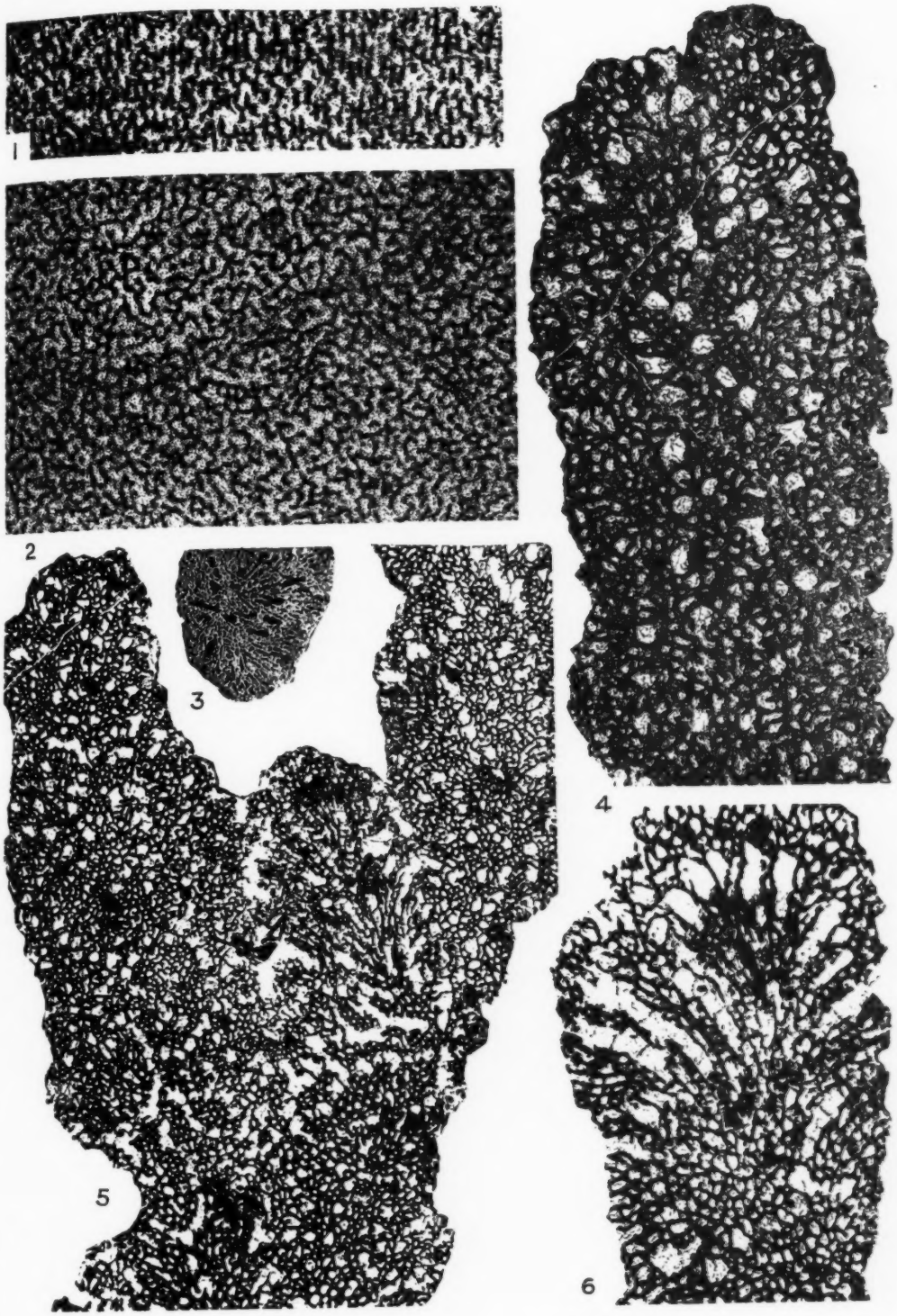
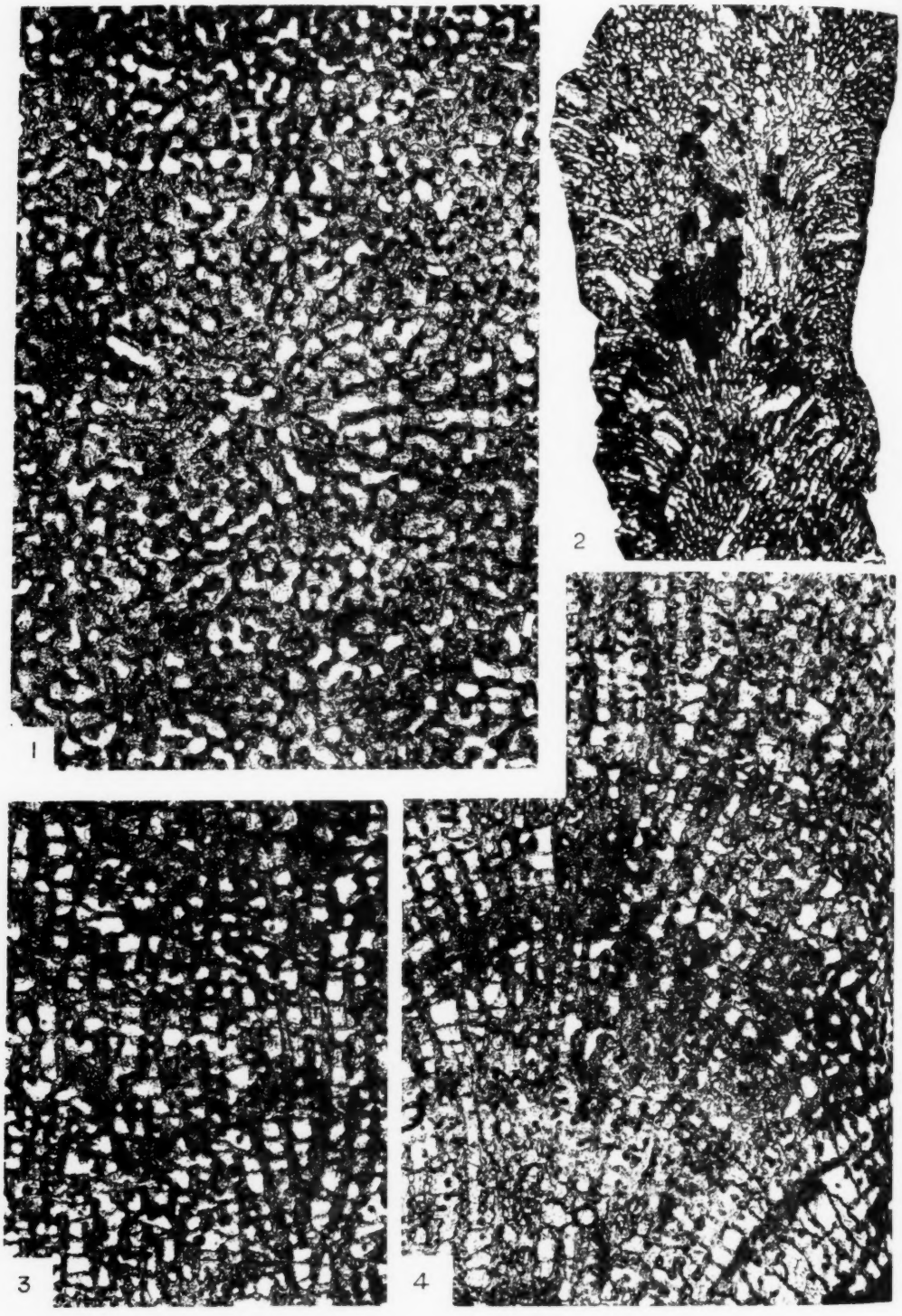
EXPLANATION OF PLATE 72

FIGS. *1, 2*—*Actinostromaria* sp. cf. *Actinostroma praesalevensis* Zuffardi-Comerci. Locality FL177. *1*, section 3B, ×9, oblique section, nearly vertical; *2*, section 3A, ×9, tangential section from nodular coenosteum, showing pillars and pillar lamellae. (p. 658)

3–6—*Milleporidium libanoticum*, Hudson n. sp. Sections from holotype. Locality FL211. *3*, section 1A (H4788A) ×3, transverse section across coenosteal branch; *4*, section 1B (H4788B), ×9, tangential section of coenosteal branch; *5*, section 1C (H4788C), ×4.5, longitudinal section of group of branches. *6*, section 1A (H4788A), ×9, oblique section, nearly vertical, showing tabulae. (p. 658)



Hudson, Jurassic stromatoporoids, Lebanon



Hudson, Jurassic stromatoporoids, Lebanon

lamellae, the whole crossed by upright tabulate astrorhizal tubes. *S. pruvosti* differs from the form described here in that the pillars are more continuous, and that individual coenosteal lamellae between the pillars are more common and more distinct.

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EXPLANATION OF PLATE 73

FIGS. *1, 3, 4*—*Parastromatopora libani* Hudson, n. sp. Sections from holotype. Locality FL209A. *1*, section 1B (H4789B), ×9, tangential section showing pillars, pillar lamellae, and astrorhizal tubes; *3, 4*, both from section 1A (H4789A), ×9; *4*, vertical, and, *3*, nearly vertical, sections showing tabulate astrorhizal tubes. (p. 659)

2—*Milleporidium libanoticum* Hudson, n. sp. Section from holotype. Locality FL211. Section 1C (H4788C), ×4.5, axial longitudinal section of branch showing major and minor tubules. (p. 658)

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BARREMIAN AMMONITES FROM TRINIDAD, B.W.I.[1]

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ABSTRACT—Some ammonites of Barremian (Early Cretaceous) age from Trinidad are described in order to establish a definite record of their presence. Many are represented by immature specimens and are therefore identified only generically. The accurate dating as Barremian of certain shales on the Pointe-à-Pierre Coast in the Central Range is useful in interpreting the geologic history of the island and of nearby parts of South America.

INTRODUCTION

SOME Barremian (Lower Cretaceous) ammonites from Trinidad are described with the permission of K. W. Barr and H. G. Kugler of Trinidad Leaseholds, Limited, who collected them. The specimens are deposited in the collections of the United States National Museum and given National Museum numbers.

These ammonites make possible accurate age determinations of certain beds that are critical in interpreting the stratigraphy and structure of the island and of adjacent parts of South America. In particular, the dating of part of the metamorphosed beds in northern Trinidad as Barremian shows that there was extensive crustal deformation of post-Barremian age in a area that is now part of the Caribbean Sea. It shows that metamorphism was not produced by orogeny earlier than the Barremian. It suggests that the metamorphosed rocks in the nearby coastal mountains of northern Venezuela are at least in part equivalent to the non-metamorphosed Cretaceous rocks farther south in Venezuela. It suggests that the metamorphism in Trinidad and Venezuela may have occurred at the same time as the latest Creteaceous to early Tertiary orogeny noted in the islands north of Venezuela (Hedberg, 1942, p. 223). These facts and implications have a bearing on the time of origin and the structural characteristics of the Caribbean Sea and, therefore, on the geologic history of the southern margin of the North American continent. The fossil evidence should be of considerable interest to many geologists studying the lands bordering the Gulf of Mexico. It is understood that the implications of the fossil evidence will be fully discussed by Messrs. Barr and Kugler in subsequent papers.

One collection, labeled BT456, consists of 145 pyritic ammonites enclosed in a low-grade phyllite matrix. It was made by K. W. Barr from the northern side of a small headland at the northern end of Tompire Bay in the Toco District, northern Trinidad, and is located by the Trinidad Government cadastral coordinates North 512,000 links, East 631,200 links. The collection includes 31 specimens of uncoiled ammonites, some of which are adults. The remainder of the collection consists of small normally coiled ammonites that are either immature or represent the inner whorls of larger ammonites. Most of the specimens are undeformed or nearly undeformed, but some were crushed before fossilization and some were distorted by chemical alterations. The fossils may be listed as follows:

Phylloceras sp., juv.
Lytoceras sp., juv.
Hamulina? sp.
Ancyloceras? sp.
Leptoceras sp. indet.
Leptoceras cf. *L. beyrichii* (Karsten)
Melchiorites sp., juv.
Barremites? sp., juv.
Saynoceras? sp., juv.
Pulchellia spp., juv.
Karstenia cf. *K. lindigi* (Karsten)
Nicklesia? sp., juv.

Another collection (K. 8187) was made by H. G. Kugler from 10 feet of calcareous, dark-gray silty shale exposed on the coast 270 feet northeast of the boat jetty at Pointe-à-Pierre in western Trinidad. The collection consists of 20 fragmentary molds of adult ammonites including five specimens of

[1] Publication authorized by the Director, U. S. Geological Survey.

Pulchellia and two of *Karstenia*. The fossils may be listed as follows:

Ancyloceras? sp.
Melchiorites? sp.
Hemihoplites? sp.
Pulchellia cf. *P. galeatoides* (Karsten)
Pulchellia sp.
Karstenia cf. *K. lindigi* (Karsten)
Karstenia sp.

The Barremian age of both of these collections is proved by the presence of *Pulchellia* and *Karstenia*, which can be identified definitely by their peculiar ornamentation. Most of the other normally coiled ammonites are questionably assigned to various genera because of poor preservation or because of their small size and nondistinctive ornamentation. Most of the uncoiled ammonites are not well enough preserved to be distinguished with confidence from other uncoiled ammonite genera of other ages in the Cretaceous or in the Late Jurassic. Consideration of the ammonites as a whole suggests that they represent the lower rather than the upper Barremian. This is indicated particularly by the presence of the pulchellids, which are characteristic of the lower Barremian (Gignoux, 1921b, p. 143), and by the absence of such genera as *Holcodiscus*, *Costidiscus*, and *Pseudohaploceras*, which are common in the upper Barremian.

A Barremian age for the phyllites at Tompire Bay at the east end of the Northern Range, according to K. W. Barr (personal communication of October 16, 1951), is in harmony with the concept that the beds in the Northern Range become younger from south to north because the Barremian locality is nearer to the Albian locality at Toco Bay (Wells, 1948; Trechmann, 1945) than it is to the latest Jurassic locality near Curare Reservoir (Spath, 1939). The Barremian age of some shales on the Pointe-à-Pierre coast was first shown by Spath (in Newton, 1924, p. 142) and is in accordance with recent studies by Kugler (1950, p. 57) and Barr (1952, p. 423) in the Central Range.

Barr (1952, p. 424) considers that the Barremian shales of the Central Range were deposited in an "open water environment—, not necessarily of great depth, but probably beyond the neritic zone." Such an environment is suggested by an abundance of the ammonite *Phylloceras*, which is common in many deposits in the Mediterrenean Province but is rare in the deposits of the shallow epeiric seas.

SYSTEMATIC DESCRIPTIONS

Genus PHYLLOCERAS Suess, 1865

PHYLLOCERAS sp., juv.
Plate 74, figures 1–3, 6, 7

This genus is the most abundant of any in the Barremian beds at Tompire Bay being represented by 72 specimens from locality BT456. Most of the specimens are moderately stout, but some are compressed. Identification is based on the suture-line, which is well preserved on some specimens.

Figured specimens.—USNM 108730.

Genus LYTOCERAS Suess, 1865

LYTOCERAS sp., juv.
Plate 74, figures 4, 5

The genus is represented by 6 specimens from locality BT456. These have a highly evolute form, a nearly circular whorl section, and bifid, nearly symmetrical lobes. The only oranamentation consists of several weak constrictions per whorl.

Figured specimen.—USNM 108729.

Genus HAMULINA d'Orbigny, 1852

HAMULINA? sp.
Plate 74, figures 21, 22, 25, 26

Locality BT456 has furnished 15 uncoiled ammonites that are characterized by gradually tapering, closely appressed limbs, by weak, nontuberculate ribbing, and by a simple suture. The sutured portion of the more slender limb is represented only by internal molds, and appears to be smooth. The body chamber, which includes the larger limb and all of the hook connecting the limbs, bears weak swellings on the hook and weak, fairly dense, posteriorly inclined ribbing on the larger limb.

The weak, dense ribbing is unlike the rather sharp, widely spaced ribbing on *Ptychoceras* (see d'Orbigny, 1842, p. 555, pl. 137, figs. 1–4), to which reference is suggested by the nearness of the two limbs. This condition of the limbs may be due to crushing however, as one specimen is not bent nearly as sharply as the others. The character of the ribbing is much more similar to

certain nontuberculate species of *Hamulina*, such as *H. paxillosa* Uhlig (1882, p. 218, pl. 14, figs. 3, 5, 6), which Gignoux (1921a, p. 128) refers to the group of *H. subcylindrica*.

Figured specimens.—USNM 108728.

Genus ANCYLOCERAS d'Orbigny, 1842
ANCYLOCERAS? sp., juv.
Plate 74, figures 19, 20

Two uncoiled ammonites from locality BT456 are tentatively referred to *Ancyloceras*. They bear straight, uniform ribs of two sizes and three rows of tubercles or swellings. On the smaller specimen the strong ribs bear weak umbilical and lateral swellings and pronounced ventral tubercles. Between successive strong ribs lie one or two weaker ribs that are nontuberculate. All ribs weaken considerably along the midventral line. On the larger specimen there is regular alternation of weak and strong ribs. The strong ribs bear three rows of acute tubercles whose strength increases ventrally. The weak ribs bear weak swellings only, corresponding in position to the tubercles on the strong ribs. The midventral line is nearly smooth. The general aspect of the ornamentation is similar to that of *Ancyloceras van-den-heckei* Astier as figured by Karsten (1858, pl. 1, figs. 2a–d).

Figured specimens.—USNM 108727.

Genus LEPTOCERAS Uhlig, 1883
LEPTOCERAS sp. indet.
Plate 74, figures 16–18

This species, represented by 10 specimens from locality BT456, differs from *Leptoceras beyrichii* (Karsten) by having much more widely spaced ribs. The ribs are high and sharp, nearly radial and are separated by interspaces from three to four times their width. They are weakened along the midventral line but are slightly thickened on the sides of the venter.

Figured specimens.—USNM 108726.

LEPTOCERAS cf. L. BEYRICHII (Karsten)
Plate 74, figures 23, 24

Four uncoiled ammonites from locality BT456 have ornamentation that appears to be identical with that of *Lepotceras beyrichi* (Karsten) (Karsten, 1858, p. 103, pl. 1, figs. 4a-d; Uhlig, 1882, p. 148, pl. 32, figs. 4–6, 8). The ribs on the flanks are rather high and sharp, incline slightly forward, and are separated by interspaces nearly twice their width. They are weakened along the midline of the venter and are thickened on the sides of the midline but are not tuberculate. The whorl section is subovate and slightly flattened on the venter.

Figured specimen.—USNM 108733.

Genus MELCHIORITES Spath, 1921
MELCHIORITES sp., juv.
Plate 74, figures 8, 9

One specimen from locality BT456 has flattened flanks, a sharpened venter, a moderately wide umbilicus, a rounded umbilical wall, and eight pronounced falciform constrictions. There are faint swellings in front of the three most anterior constrictions. Ribbing is not visible.

Figured specimens.—USNM 108732.

Genus BARREMITES Kilian, 1913
BARREMITES? sp., juv.
Plate 74, figures 10–15

Ten ammonites from locality BT456 rep-

EXPLANATION OF PLATE 74

All figures twice natural size unless otherwise indicated.

All specimens from locality BT456 at northern end of Tompire Bay.

FIGS. *1–3, 6, 7—Phylloceras* sp., juv. *1*, lateral view showing sutures. USNM 108730a; *2, 3*, lateral and ventral views, USNM 108730b; *6, 7*, lateral and ventral views, USNM 108730c. (p. 663)

4, 5—Lytoceras sp., juv. Lateral and ventral views, USNM 108729. (p. 663)

8, 9—Melchiorites sp., juv. Lateral and ventral views, USNM 108732. (p. 664)

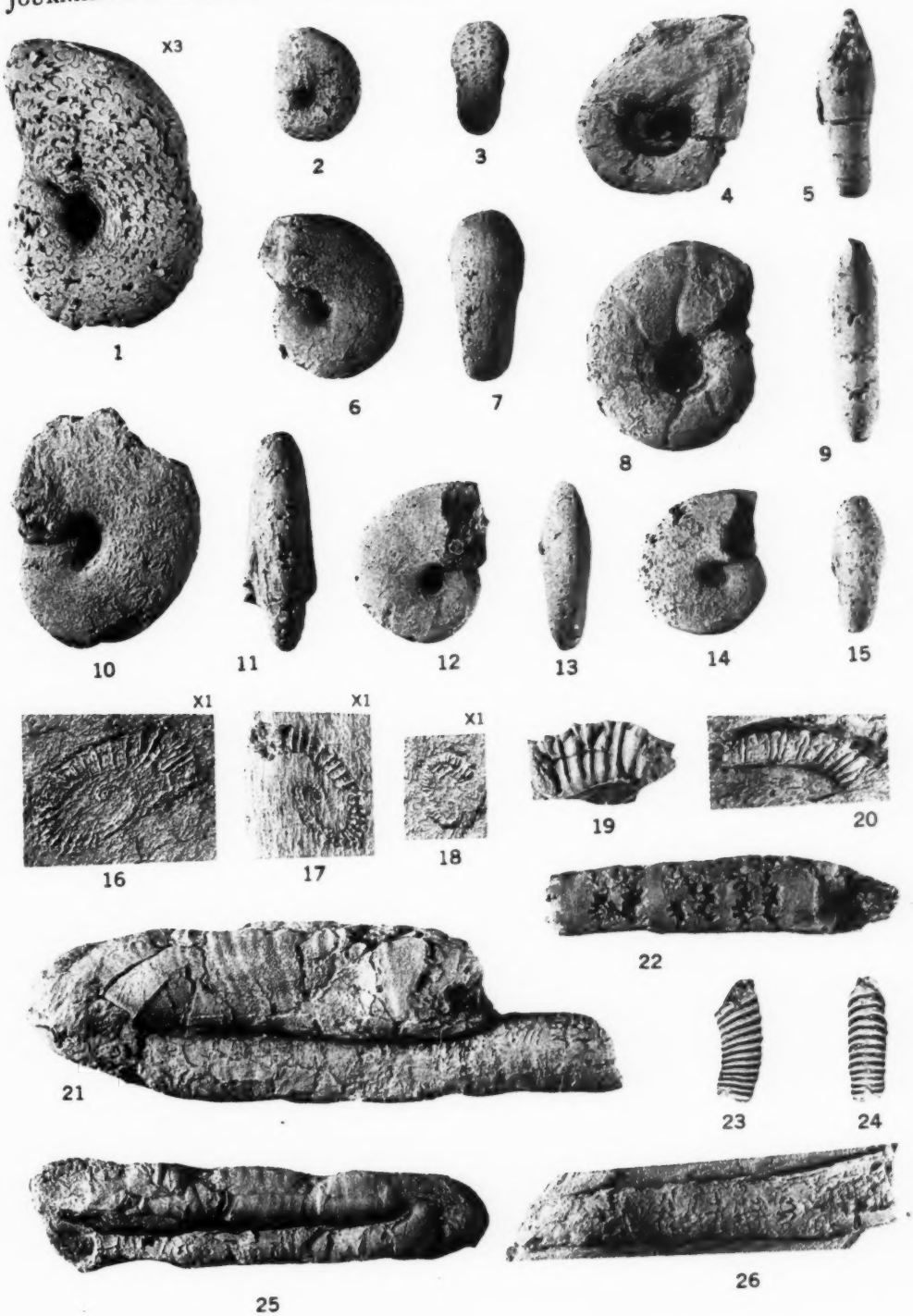
10–15—Barremites? sp., juv. *10, 11*, lateral and ventral views, USNM 108731a; *12, 13*, USNM 108731b; *14, 15*, USNM 108731c. (p. 664)

16–18—Leptoceras sp. indet. Lateral views USNM 108726. (p. 664)

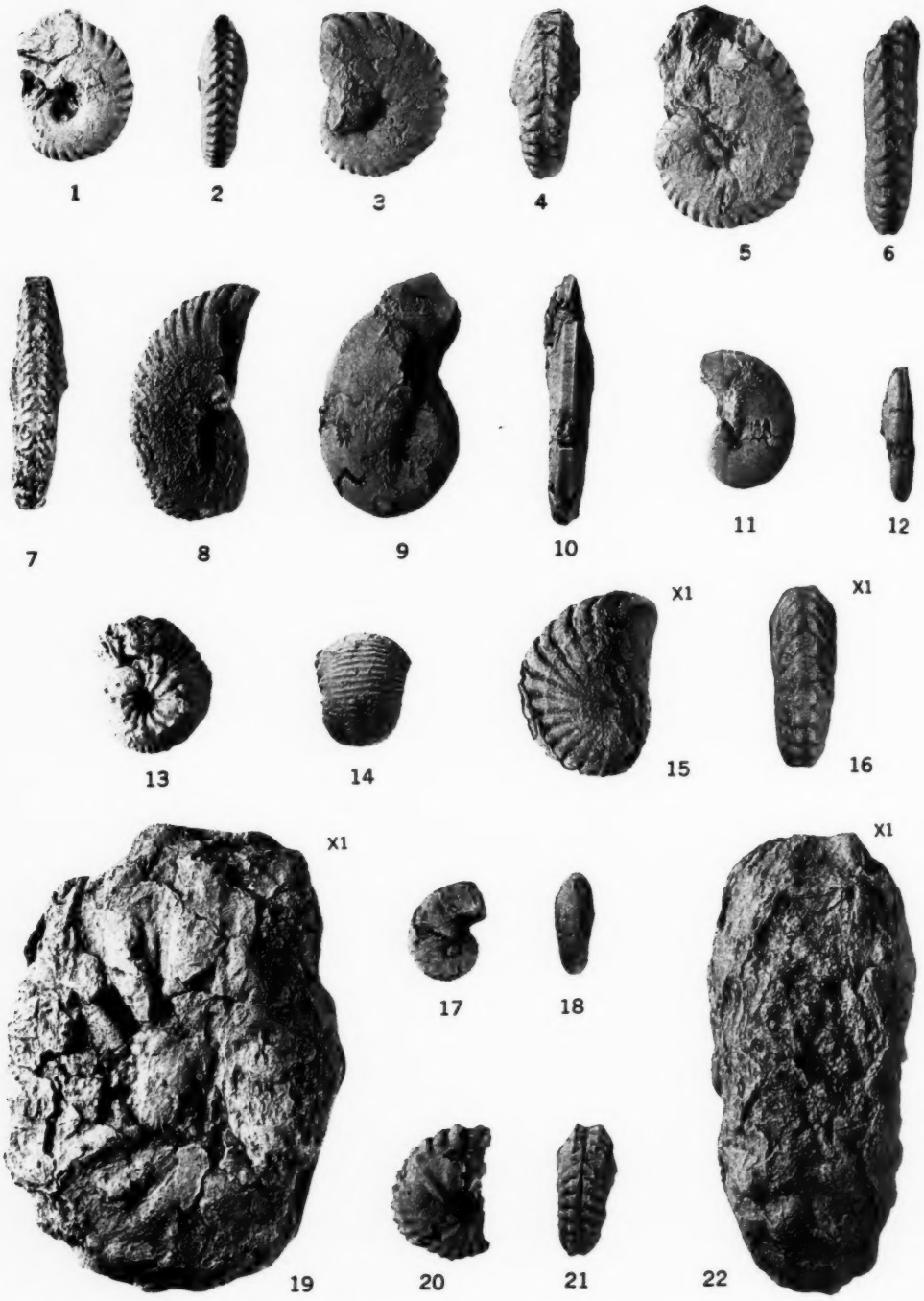
19, 20—Ancyloceras? sp., juv. Lateral views of two specimens, USNM 108727. (p. 664)

21, 22, 25, 26—Hamulina? sp. *21, 25*, lateral views showing hook and weakly ornamented body chamber; *22, 26*, lateral views showing sutures. USNM 108728. (p. 663)

23, 24—Leptoceras cf. L. *beyrichii* (Karsten). Lateral and ventral views, USNM 108733. (p. 664)



Imlay, Trinidad Barremian ammonites



Imlay, Trinidad Barremian ammonites

resent immature desmoceratids. They have flattened flanks, a narrowly rounded venter, a narrow umbilicus, and a low, vertical umbilical wall. Some of the specimens are a little stouter than others. Under oblique lighting some of the specimens show faint, forwardly inclined constrictions but no trace of ribbing. Considering the small size of the specimens and their lack of distinctive features, the generic assignment is highly uncertain. Their association with Barremian pulchellids suggests that they probably belong to such genera as *Barremites* or *Pseudohaploceras*.

Figured specimens.—USNM 108731.

Genus SAYNOCERAS Munier-Chalmas, 1893

SAYNOCERAS? sp., juv.

Plate 75, figures 13, 14

One ammonite from locality BT456 is represented by the penultimate whorl and about one-third of the body whorl. The body whorl was crushed and healed during the life of the animal and was crushed again later, presumably before fossilization. The penultimate whorl is not deformed.

The ammonite is small, involute, globose; the whorl is depressed ovate in section, much wider than high. The venter is broadly rounded, and the flanks are narrow. The umbilicus is narrow and deep; the umbilical wall is high, vertical at base, rounding evenly above.

The penultimate whorl has 13 primary ribs and about 56 secondary ribs. The primary ribs begin low on the umbilical wall, are high and rather narrow, curve forward strongly on the flanks, and terminate in acute lateral tubercles. Both primary ribs and tubercles become markedly stronger anteriorly. From the tubercles pass bundles of two to three ribs. Between these are one or two secondary ribs that arise along the zone of tuberculation. All secondary ribs cross the venter transversely or with a slight backward arching along the midventral line.

The sculpture on the posterior part of the body chamber differs from that just described by being considerably stronger. There is no evidence for the presence of ventral tubercles or of zigzag ribbing as in the adult *Saynoceras*.

The specimen is evidently immature and at a stage of development similar to immature forms of *Olcostephanus*, *Astieridiscus*, or *Holcodiscus*. Assignment to *Saynoceras* rather than to these genera is based on the prominence of the primary ribs and of the lateral tubercles, on the marked stengthening of these features anteriorly, on the depressed whorl section, and on the fairly small umbilicus. Comparable immature specimens of *Holcodiscus* (Fallot and Termier, 1923, pl. 4, figs. 7–9, pl. 5, figs. 3, 7–12) are more evolute, thinner, and have less regular tuberculation. *Astieridiscus* is much more compressed and has much weaker primary ribs. *Olcostephanus* does not develop so prominent primary ribs or tubercles at such a small size and is generally more evolute.

Figured specimen.—USNM 108734.

Genus PULCHELLIA Uhlig, 1883

PULCHELLIA cf. P. GALEATOIDES (Karsten)

Plate 75, figures 15, 16

One specimen form locality K8187 on the

EXPLANATION OF PLATE 75

All figures twice natural size unless otherwise indicated.
Specimens shown as figures 1–18 are from locality BT456.
Specimens shown as figures 19–22 are from locality K8187.

FIGS. *1–6*—*Pulchellia* sp., juv., cf. *P. selecta* Gerhardt. Lateral and ventral views of three specimens, USNM 108737. (p. 666)

7, 8—*Pulchellia* sp., juv., cf. *P. multicostata* Riedel. Ventral and lateral views, USNM 108735. (p. 666)

9–12—*Pulchellia* sp., juv., cf. *P. compressissima* (D'Orbigny). Lateral and ventral views, USNM 108736. (p. 666)

13, 14—*Saynoceras*? sp., juv. Lateral and ventral views, USNM 108734. (p. 665)

15, 16—*Pulchellia* cf. *P. galeatoides* (Karsten). Lateral and ventral views, USNM 108724. (p. 665)

17, 18—*Nicklesia* sp., juv. Lateral and ventral views, USNM 108739. (p. 667)

19–22—*Karstenia* cf. *K. lindigi* (Karsten). *19, 22*, lateral and ventral views of adult specimen, USNM 108725; *20, 21*, lateral and ventral views of immature specimen, USNM 108738. (p. 666)

Pointe-à-Pierre coast has very broad ribs that begin at or near the umbilicus, incline forward gently on the lower part of the flanks, bend forward considerably near the venter, and terminate in spirally elongate tubercles that bound a smooth midventral area. At a diameter of 25 mm., the whorl height is 15 mm. and the whorl thickness is 9 mm. The stoutness of the specimen suggests comparison with *P. galeatoides* (Karsten) (1858, p. 107, pl. 3, figs. la, b; Collet, 1924, p. 491 pl. 15, figs. 8, 12, 12a; Riedel, 1938, p. 66, pl. 11, figs. 8, 9) rather than with *P. galeata* (von Buch) (d'Orbigny, 1842, p. 32, pl. 2, figs, 3–5; Roschen, 1929 p. 25, pl. 7, fig. 9, pl. 8, figs. 5, 6) or *P. veleziensis* Hyatt (Gerhardt, 1898, p. 145, pl. 3, fig. 4; Roschen, 1929, p. 38, pl. 5, figs. 1–4), which species have similar ribbing.

Figured specimen.—USNM 108724.

PULCHELLIA spp., juv.
Plate 75, figures 1–12

The collections from the Tompire Bay locality include 22 specimens of *Pulchellia*, of which the largest is only 15 mm. in diameter. These specimens are readily separable into three morphological groups, which may represent species, but specific identification cannot be made because the specimens are much smaller than any of the illustrations of described species and the comparative material in the collections of the U. S. Geological Survey includes only much larger specimens.

The most common group (pl. 75, figs. 1–6), represented by 19 specimens from locality BT456 may be compared with *Pulchellia selecta* Gerhardt (1898, p. 142, pl. 3, figs. 2a, b; Collet, 1924, p. 490, pl. 15, figs. 9, 9a, 10, 10a) because of the presence of rather strongly falciform, broad ribs; but comparison with similar species such as *P. hettneri* Gerhardt (1898, p. 144, pl. 3, figs. 3a, 3b) or *P. galeatoides* Karsten (1858, p. 107, pl. 3, figs, la, 1b; Gerhardt 1898, p. 147, pl. 3, fig. 5; Riedel, 1938, p. 66, pl. 2, figs. 8, 9) might be just as apt.

Two small specimens (pl. 75, figs. 9–12) from locality BT456 have a much compressed whorl section, an extremely narrow umbilicus, a flattened to slightly concave venter bordered by low ridges and only faint traces of forwardly inclined ribbing. These features suggest that the specimens may be immature forms of *P. compressissima* (d'Orbigny, 1841, p. 210, pl. 61, figs. 4, 5; Karsten, 1858, pl. 2, figs. 9a, b; Gerhardt, 1898, p. 140, pl. 3, figs. 1a, b).

One specimen (pl. 75, figs. 7, 8) from locality BT456 is characterized by fine, closely spaced ribbing. This feature suggests comparison with *P. multicostata* Riedel (1938, p. 68, pl. 2, figs. 21, 22).

Figured specimens.—USNM 108735, 108736, 108737.

Genus KARSTENIA Hyatt, 1903
KARSTENIA cf. K. LINDIGI (Karsten)
Plate 75, figures 19–22

The genus is represented by three specimens from Trinidad. One internal mold (pl. 75, figs. 19, 22) from locality K8187 measures 64 mm. in maximum diameter and at the anterior end has a whorl thickness of 31 mm. and a whorl height of about 33 mm. It bears a row of weak tubercles low on the flanks and two rows of rather prominent tubercles on each side of the venter. The latter is marked by a distinct furrow. The stoutness and ornamentation of the specimen is similar to that of some previously illustrated specimens of *Karstenia lindigi* (Karsten) (1858, p. 108, pl. 3, figs. 3a, b; Collet, 1924, pl. 15, figs. 1, 1a).

Two immature specimens (pl. 75 figs. 20, 21) of *Karstenia* from locality BT456 are much smaller than any published figures of the genus but show the essential features very well. The specimen illustrated has strong, widely spaced primary ribs that begin at or near the base of the umbilical wall, then incline forward and give rise to weak tubercles a little below the middle of the flanks. From the tubercles pass two secondary ribs that become broader ventrally. One or two secondary ribs arise independently on the flanks between the forked ribs. All ribs bear two rows of tubercles on each side of the venter. Of these the ventral row is much stronger. At the posterior end of the specimen the tubercles are nearly conical, but anteriorly they become spirally elongated. The venter is marked by a deep, narrow furrow that channels both ribs and interspaces.

Figured specimens.—USNM 108725, 108738.

NICKLESIA? sp., juv.
Plate 75, figures 17, 18

One small specimen from locality BT456 is referred doubtfully to *Nicklesia* because of the presence of very broad, slightly flexuous ribs that are continuous across a narrowly rounded venter. The assignment is influenced by the presence of other pulchellids at the same locality.

Figured specimen.—USNM 108739.

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QUANTITATIVE STUDIES OF BRACHIOPODS FROM THE LOWER CARBONIFEROUS REEF LIMESTONES OF ENGLAND. III. *PUGNAX ACUMINATUS* (J. SOWERBY) AND *P. MESOGONUS* (PHILLIPS)

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ABSTRACT—*P. acuminatus* is a variable species both in ornament and shape. The variants do not seem to have time value, though the typical form is commoner at the higher than the lower stratigraphical horizons. Relative growth is allometric, with a change in the growth ratio at a width of 25 mm.

P. mesogonus is separated specifically from *P. acuminatus*. It exhibits less variability than the latter form.

INTRODUCTION

Pugnax acuminatus (J. Sowerby) is one of the most variable forms among the brachiopods of the Lower Carboniferous reef limestones. Davidson's interpretation of the species included J. de C. Sowerby's varieties *P. a. plicatus* and *P. a. sulcatus*, *P. platylobus* (J. de C. Sowerby) and *P. mesogonus* (Phillips).

Davidson's very numerous figures (1860, pls. 20, 21) include a great variety of forms. An early investigation by the author (Parkinson, 1926) suggested the possibility that *P. sulcatus* might be specifically distinct from *P. acuminatus*, *P. plicatus* being regarded as a variety of *P. acuminatus* and *P. platylobus* as a variety of *P. sulcatus*. Phillips' species *P. mesogonus* (1836, p. 222; pl. 12, figs. 10, 11, 12) was considered to be valid. The possibility was also suggested of a phylogenetic change from *P. a.* var. *plicatus* to the type *P. acuminatus*.

The work reported in the present paper is mainly of a biometric character, upwards of 1,000 specimens having been inspected, of which about 700 were measured and 285 submitted to statistical examination. These include specimens from the *Caninia* and *Dibunophyllum* zones but not from the intervening *Seminula* zone.

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GENERAL CHARACTERS OF *Pugnax acuminatus* s. l.

The rhychonellid shells comprising this group vary mainly in the contour of the anterior margin and in the ratio of the thickness to the length and width of the shell. A preliminary examination of the large and varied material available indicated that the author's former conclusion (1926) that *P. mesogonus* is a species distinct from *P. acuminatus* was justified, but the further suggestion that *P. sulcatus* might also be regarded as a separate species had to be discarded since, although the typical form of *P. a.* var. *sulcatus* (J. de C. Sowerby 1812–29, vol. 5, p. 153; pl. 495, fig. 1) is quite distinct from the type *P. acuminatus* in the nature of the anterior margin, the two forms grade into each other by a series of intermediates, J. de C. Sowerby's variety *P. a. plicatus* (1812–29, vol. 5, p. 153 and pl. 495, fig. 3) being one of these. The flattened form *P. platylobus* (J. de Sowerby 1812–29, vol. 5, p. 155; pl. 496, figs. 5, 6) cannot be regarded as other than an extreme form of *P. a.* var. *sulcatus*. The plicated variants comprise innumerable varieties of "acuminate" and "sulcate" forms.

The lectotype of *P. acuminatus* (J. Sowerby, 1822) is figured by Muir-Wood (1951, pl. 3, figs. 1a, 1b, 1c). It is a smooth

form with the apex of the anterior margin acute but not quite pointed. There are no costae or plications.

The internal characters of *P. acuminatus* are similar to those of *P. pugnus* (Weller, 1914, p. 202) but the crura in the brachial valve, which are no more than the enlarged inner ends of the divided hinge plate in *P. pugnus* are somewhat better developed in *P. acuminatus*. Dr. Muir-Wood has shown the writer photographs of several sections passing through the umbonal region of *P. acuminatus* which agree with his own observations on a number of specimens. Davidson (1860, pl. 20, fig. 6) figures an interior of the brachial valve.

The essential difference between species of *Pugnax* and those of other Lower Carboniferous rhychonellid genera is in the absence of a medium septum in the brachial valve of *Pugnax*. Some specimens of *P. acuminatus* and *P. pugnus* (Parkinson, 1954b) have a thin septal ridge which is quickly removed by grinding the valve.

BASIS OF THE STATISTICAL STUDY

It soon became evident that unlike the case of *P. pugnus* (Parkinson, 1954b) use could not be made of the number of plications and costae in comparing collections. Many specimens are quite smooth and many have well-defined costae; in many the costae are no more than slight wrinkles and the actual number of costae present in a given individual often becomes a matter of opinion. These points are brought out to some extent in figures 1 and 2, but more convincingly in the many examples figured by Davidson (1860, pls. 20, 21) a number of the originals of which have been examined by the author.

The characters considered are the length L, the width W and the thickness T, measured at right angles to the length through the middle of the shell. The total thickness or depth D has also been measured, but D is closely correlated with T and as its statistics have not added anything of value they are excluded from the paper. The meaning of the symbols L, W, T and D is clear from figure 1.

Specimens have been examined and measured from many localities, and five collections representing three stratigraphical levels have been submitted to quantitative analysis. The largest assemblage (250 measured specimens from the Craven Reef Belt, Yorkshire, in the *Dibunophyllum* zone and housed in the Tiddeman collection of Skipton Museum) was excluded because of suspected non-randomness. Separation had been made into different groups and the impression was gained that a number of specimens were missing. However, the collection proved valuable in showing the nature and extent of variation (fig. 2) and the same can be said of upwards of 100 specimens in the British Museum (Natural History) and Geological Survey collections from "Bolland" a belt of country on the borders of Lancashire and Yorkshire. Thirty-five specimens from the Manchester Museum labelled "Thorpe, near Skipton" in the Craven Reef Belt are strongly reminiscent of the Clitheroe reefs and as a group are unlike the Tiddeman collection. In no respects in fact do they differ significantly from the Salt Hill (C_2 zone) assemblage and the possibility exists that they may have come from Clitheroe and are wrongly referred to Thorpe. They have therefore been discarded.

Of the five collections biometrically compared only one, from C_2 of Thorpe Cloud, Derbyshire, near the entrance of Dovedale, can be regarded as approximating to an interbreeding community. These 93 specimens come from a few inches of strata at the northern end of the ridge forming the summit of Thorpe Cloud (Parkinson, 1950a).

The next nearest approach to a community in the strict sense is the Withgill (near Clitheroe, Lancashire) assemblage which ranges through 30 feet or so of C_2 reef facies at the top of the Clitheroe Limestone (Parkinson, 1954a). The collection from Salt Hill and Bellman quarries, Clitheroe, has a much wider range at the same general level as Withgill. However, although some 400 feet of reef limestones are exposed in these quarries they represent no more than the upper third of the C_2 zone (Parkinson 1950b).

The reef limestone of Coplow knoll, Clitheroe is the lowest horison (upper C_1) represented. It has a maximum thickness of upwards of 400 feet (Parkinson, 1950b). The collection from here is unfortunately a small one.

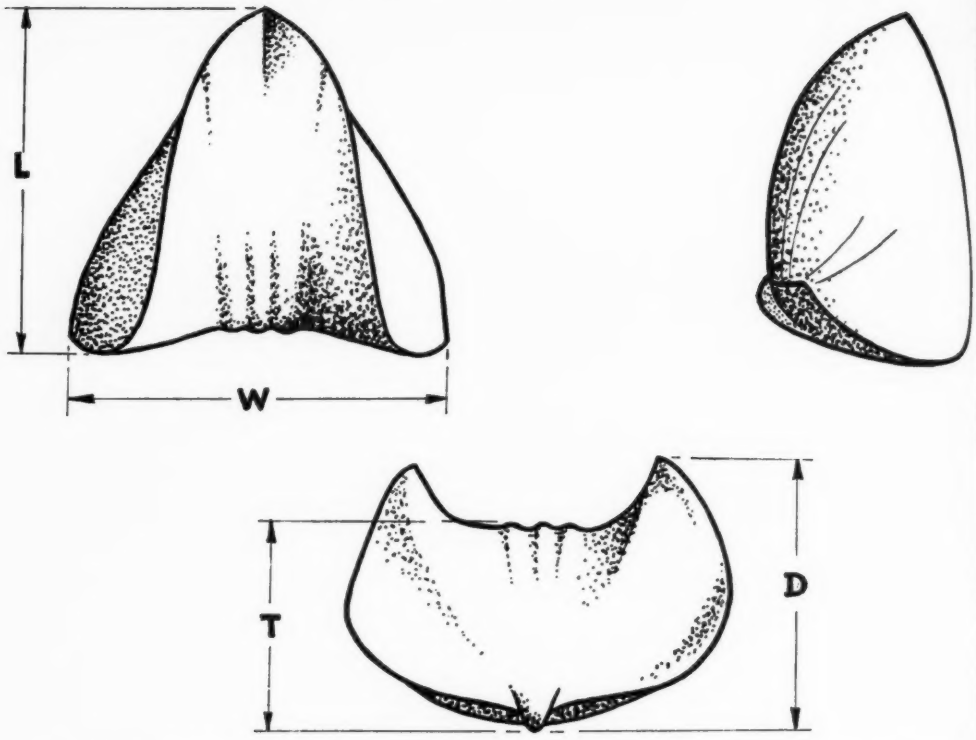

FIG. 1—Three views of same specimen of *Pugnax acuminatus*, Withgill quarry, near Clitheroe Lancashire. Natural size. D.P. coll.

The assemblage from D_{1-2} of Narrowdale Hill, Staffordshire, is fairly well localised. It includes specimens from the Geological Survey and British Museum (National History) collections in addition to those gathered by the author. The thickness of the strata from which the material was derived has not been ascertained because of the unbedded nature of the reef limestone, but it is probably not considerable.

COMPARISON OF THE COLLECTIONS

Previous work on brachiopods (Parkinson, 1954a, 1954b) has shown that in comparing populations ratios of metrical characters are useful unless growth is far removed from isometric, but where applicable it is better to determine the relation between the dimensions either by simple regression (Parkinson, 1952) or by Kermack and Haldane's reduced major axis method (1950). The latter method, which involves less computation than regression and makes unnecessary any artificial distinction between independent and dependent variates, has been employed in the present study.

Particulars of the collections of *P. acuminatus*, together with the average dimensions of the shells from each locality, are given in Table 1. It is seen that size varies according to location, but not with stratigraphical level.

TABLE 1.—DATA ON COLLECTIONS OF *P. acuminatus*

L = length W = width T = thickness
N = number of specimens

Locality	Zone	N	Mean Dimensions mm.		
			L	W	T
Coplow	C_1	17	25.3	29.0	16.5
Salt Hill	C_2	53	27.8	32.7	17.4
Withgill	C_2	64	32.3	38.4	20.0
Thorpe Cloud	C_2	93	20.7	25.9	10.9
Narrowdale	D_{1-2}	58	27.8	32.6	16.8

In figure 3 length is plotted against width on arithmetical coordinates of *P. acumina-*

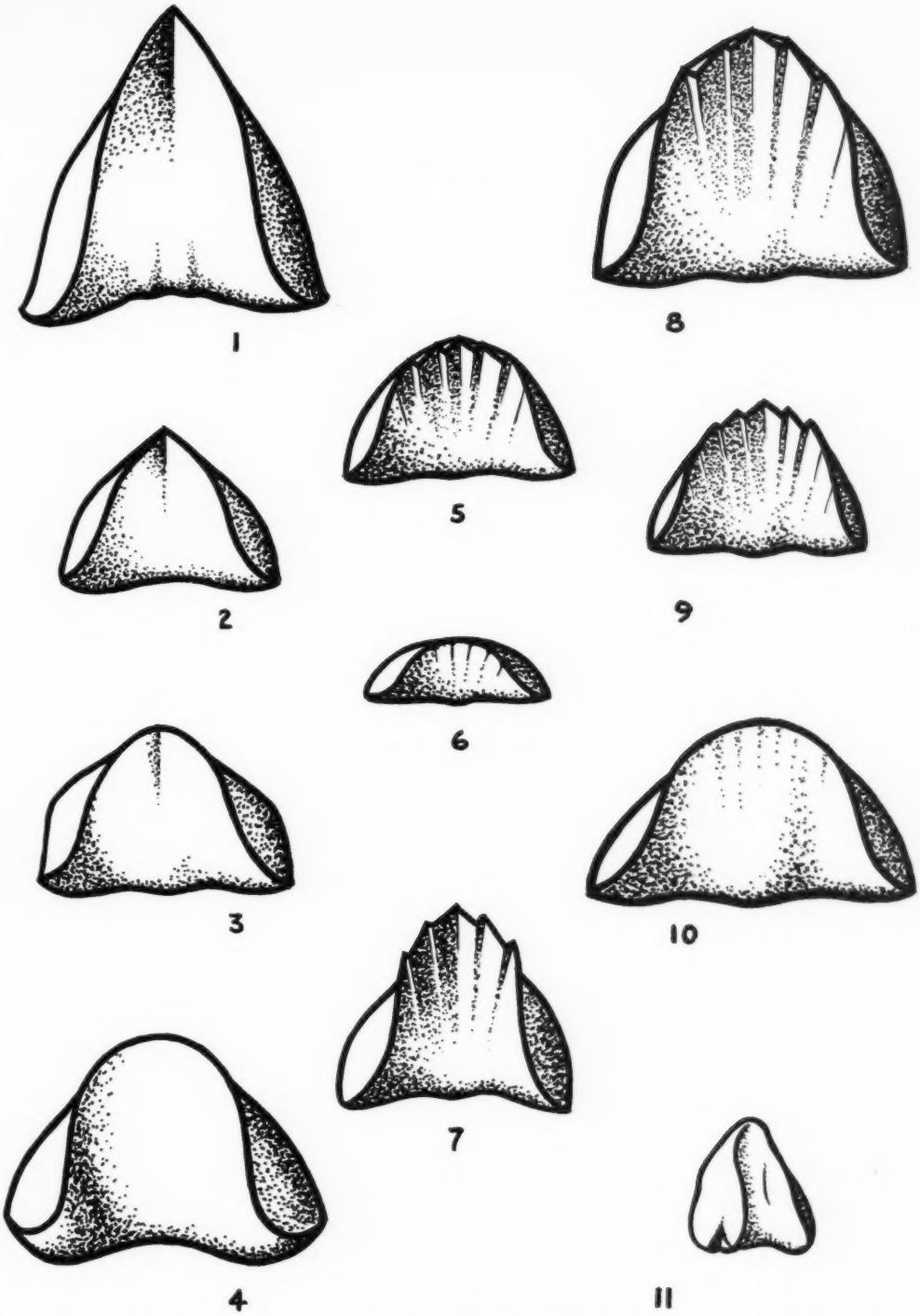

FIG. 2—Ventral views of *P. acuminatus* illustrating the range of variation. *1–7*, Tiddeman coll., Skipton Museum; *8–10*, Withgill quarry, near Clitheroe. D.P. coll. *11*, oblique view of *P. mesogonus*, Fort coll., Clitheroe. All natural size.

tus of all the specimens cited above and also for *P. mesogonus*. (The latter species is considered later.) The scatter (ignoring the points representing *P. mesogonus*) is slightly curved, suggesting that relative growth is not quite isometric when all localities and horizons are taken as a whole. The ratio L/W tends to increase as growth proceeds. The diagram illustrates the range in sizes from the different localities. At Withgill the species attained a greater size than elsewhere.

Thickness is plotted against width in figure 4. The scatter (again ignoring *P. mesogonus*) is markedly curved, showing a departure from isometry and an increase in the T/W ratio with increasing growth.

In figure 5 length is plotted against width on logarithmic coordinates for the interbreeding community of Thorpe Cloud. There is a bend in the scatter at a width of about 25 mm. This is even more pronounced in figure 6 which relates thickness to width for the same community. The analyses were therefore made separately for the specimens below and above 25 mm. in width and it is seen that the Kermack and Haldane lines pass centrally through the points. This indicates that growth is allometric with a change in the growth ratio at 25 mm. width.

TABLE 2. EQUATIONS EXPRESSING RELATIONS BETWEEN L AND W AND T AND W

Thorpe Cloud W<25 mm.	
$L=0.937\ W^{0.961}$	Log L=0.951 log W−0.028
$T=0.123\ W^{1.335}$	Log T=1.335 log W−0.912
Narrowdale. W<25 mm.	
$L=0.656\ W^{1.060}$	Log L=1.060 log W−0.183
$T=0.0333\ W^{1.799}$	Log T=1.799 log W−1.477
Thorpe Cloud. W>25 mm.	
$L=0.556\ W^{1.104}$	Log L=1.104 log W−0.255
$T=0.0226\ W^{1.873}$	Log T=1.873 log W−1.646
Narrowdale. W>25 mm.	
$L=0.403\ W^{1.209}$	Log L=1.209 log W−0.395
$T=0.0798\ W^{1.525}$	Log T=1.525 log W−1.098
Withgill. W>25 mm.	
$L=0.697\ W^{1.050}$	Log L=1.050 log W−0.157
$T=0.197\ W^{1.264}$	Log T=1.264 log W−0.705.
Salt Hill. W>25 mm.	
$L=0.794\ W^{1.020}$	Log L=1.020 log W−0.100
$T=0.178\ W^{1.314}$	Log T=1.314 log W−0.749
Coplow. W>25 mm.	
$L=0.0692\ W^{1.071}$	Log L=1.071 log W−1.160
$T=0.294\ W^{1.044}$	Log T=1.044 log W−0.531.

Subsequent analyses were all made on this basis (figs. 7 to 12 and Table 2). At Salt Hill, Withgill and Coplow there are few specimens less than 25 mm. in width and the analyses have been confined to the larger size groups. Because of the small size of the Coplow sample a plot has not been made, but the equations of the K and H lines are given in Table 2. The diagrams show a wider scatter of points for the T-W than for the L-W plots in line with earlier work on brachiopods (Parkinson, 1954a, b).

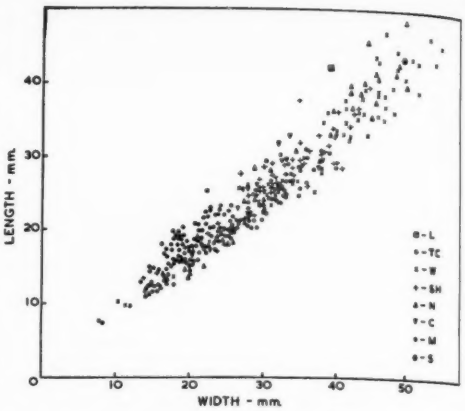

FIG. 3—Relation of length to width. M represents *P. mesogonus*, various localities. Other symbols represent *P. acuminatus;* L, lectotype, British Museum (Nat. Hist.) Sowerby Coll., B61235; TC, Treak Cliff; W, Withgill; SH Salt Hill; N, Narrowdale; C, Coplow; S, cf. *P. mesogonus*, Sheffield Univ. coll.

Tests of significance (not including the small Coplow sample, the randomness of which is doubtful) applied to the L-W equations (W>25 mm.) indicates that all the samples might have been drawn from the same population. This is not the case for the T-W equations. Withgill, Salt Hill and

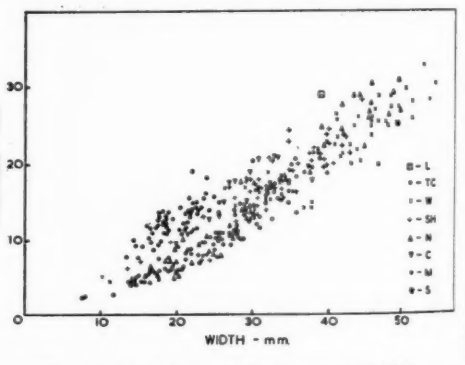

FIG. 4—Relation of thickness to width. Symbols as for figure 3.

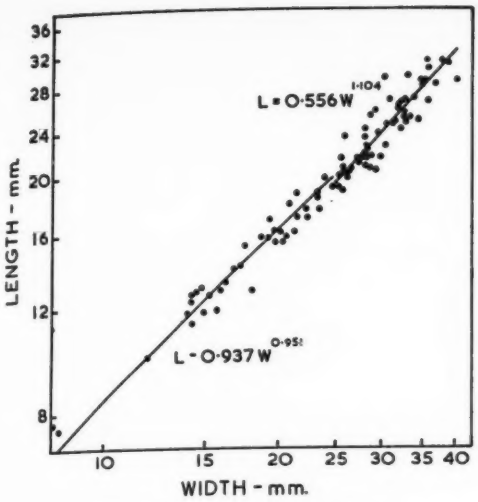

FIG. 5—Relation of L to W, Thorpe Cloud, Derbyshire.

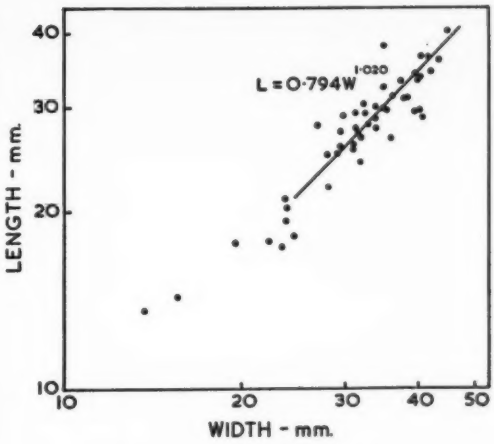

FIG. 8—Relation of L to W, Salt Hill, Clitheroe.

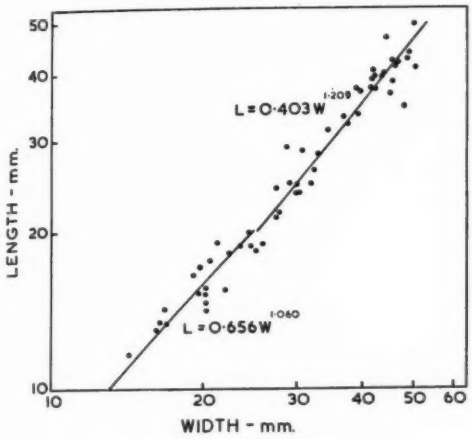

FIG. 6—Relation of L to W, Narrowdale, Staffordshire.

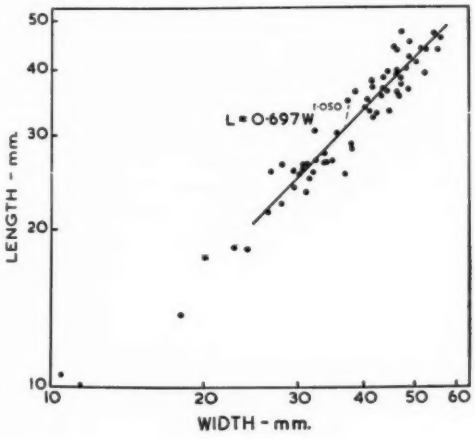

FIG. 7—Relation of L to W, Withgill, near Clitheroe, Lancashire.

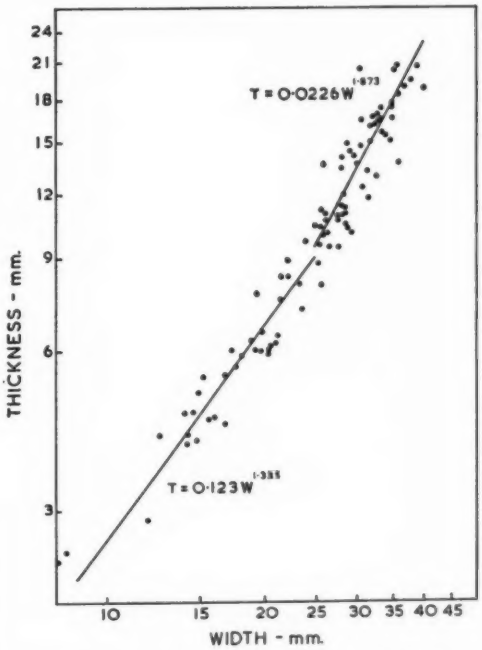

FIG. 9—Relation of T to W, Thorpe Cloud.

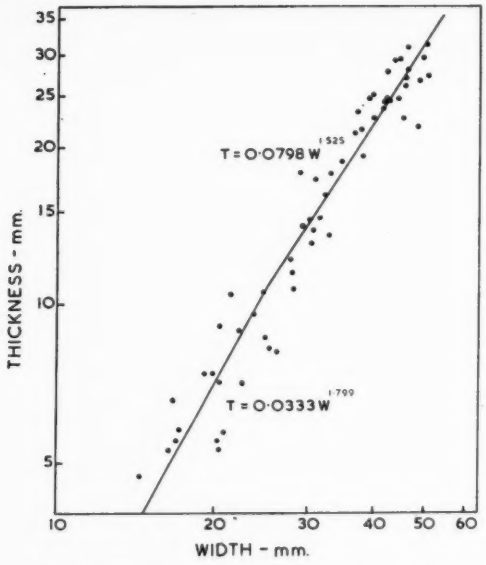

FIG. *10*—Relation of T to W, Narrowdale.

Narrowdale do not differ significantly from each other, but Thorpe Cloud differs significantly at the 1% level of probability from Salt Hill and Withgill, though not from Narrowdale. It is evident that these differences are not concerned with differences in stratigraphical horizon, since

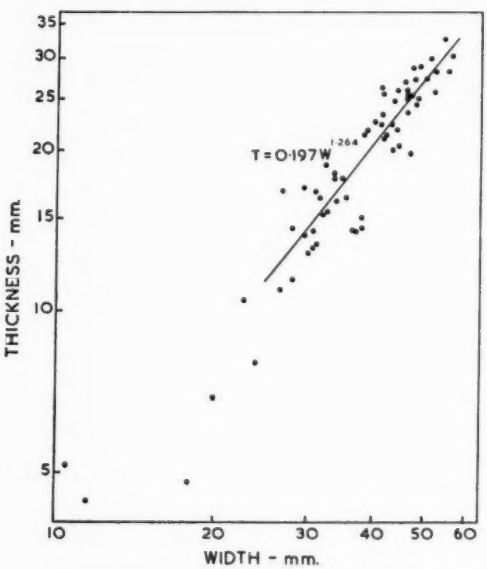

FIG. *11*—Relation of T to W, Withgill.

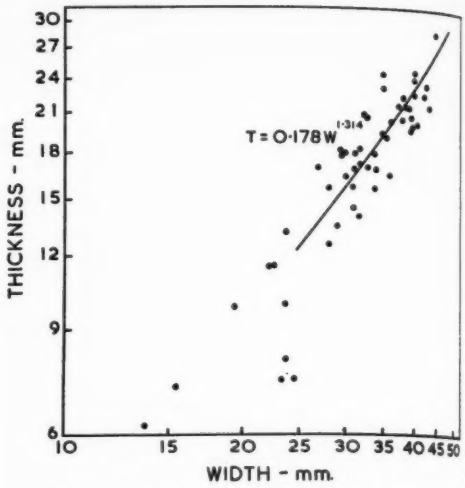

FIG. *12*—Relation of T to W, Salt Hill.

Thorpe Cloud is approximately at the same level as Salt Hill and is much lower than Narrowdale.

The inference is therefore that the relationship between L and W is dependent neither on locality nor horizon, but that T varies with W according to locality, there being no indication of phylogenetic change through the *Caninia*, *Seminula* and *Dibunophyllum* zones.

There remains the possibility of evolutionary change in respect of plication and costation as formerly suggested (Parkinson, 1926). This aspect of the investigation has not proved amenable to statistical treatment; nevertheless it does appear that the plicated forms are relatively more numerous in the lower zones than in the higher ones, and further, that the unplicated form with the acutely pointed anterior margin (1 in fig. 2) is uncommon in the C reefs and common in the D reefs. But this does not necessarily mean a phylogenetic trend from the plicate to the acuminate forms since the differences could be ecological. In this respect it is interesting to note that about half the specimens in a combined small collection in the Geological Survey and Natural History museums from Little Island, County Cork, Eire, are acuminate unplicated forms.

Pugnax mesogonus (PHILLIPS)

A former study (Parkinson, 1926, 235–9; pl. 14) indicated that Phillips' species was

distinct from *P. acuminatus*. The 100 or so specimens from Salt Hill and Bellman quarries, Clitheroe, on which this view was based have unfortunately been lost, but a further 57 specimens, many of them from the Clitheroe quarries, have been measured during the course of the present work, and the earlier conclusion has been amply confirmed. Number 11 of figure 2 is a typical form of the species which differs from *P. acuminatus* in its smaller size and in the presence of one (occasionally two) plications on each flank near the opening of the sinus. A further difference is in the larger L/W and T/W mean ratios. This is brought out clearly in figures 3 and 4, where points representing *P. mesogonus* lie mostly above those for *P. acuminatus*.

P. mesogonus is characteristic of the C_2 reef limestones, particularly at Salt Hill, Clitheroe. It is rare in the D knolls and altogether is a less common species than *P. acuminatus*.

The asterisk in figures 3 and 4 denotes an interesting specimen from the Sheffield University collection. This resembles a giganteid *P. mesogonus* in the presence of a plication on each ear, the position, size and shape of which in relation to the size of a shell are in the right proportion for *P. mesogonus*. It is thought however, that this specimen should be referred to *P. acuminatus*. It is so large that it seems unlikely that it can be an over-grown *P. mesogonus*. The position indicating it in figures 3 and 4 is quite remote from the cluster of points representative of *P. mesogonus*.

FORM OF THE DISTRIBUTIONS

Plots on probability paper (not reproduced) have indicated that for the interbreeding community of *P. acuminatus* at Thorpe Cloud the three dimensions, L. W and T are very roughly normally distributed, but similar plots for Narrowdale do not indicate a normal distribution. The L/W ratios of all assemblages of *P. acuminatus* tested give straight lines on logarithmic probability paper indicating lognormal distributions. This seems to be usual in brachiopods (Parkinson, 1954a, b) but lognormality is not the general rule for the T/W and T/L distributions, though these have been found to be lognormal in some cases. For *P. acuminatus* as in other species of *Pugnax* the T/W distribution is neither normal nor lognormal.

CONCLUSIONS

These may be summarized as follows:

(1) *P. acuminatus* and *P. mesogonus* are distinct species. (Davidson considered *P. mesogonus* to be a variety of *P. acuminatus*.)

(2) *P. platylobus*, *P. sulcatus* and *P. plicatus* are all varieties of *P. acuminatus* as envisaged by Davidson.

(3) *P. mesogonus* is a more uniform species than *P. acuminatus*.

(4) *P. acuminatus* shows considerable variation at all stratigraphical levels.

There is similar relationship between length and width for all assemblages subjected to statistical treatment.

The thickness-width relationship shows significant differences between some of the collections. These differences are unrelated to stratigraphical levels.

Variation in ornament is characteristic of all horizons, the sharply acuminate unplicated forms being particularly characteristic of the higher reefs. This does not necessarily indicate phylogenetic change.

(5) Relative growth in *P. acuminatus* is allometric, there being evidence of a change in the growth ratios at a width of shell of approximately 25 mm.

(6) The L/W ratios of *P. acuminatus* are lognormally distributed in common with those of other brachiopods previously studied.

(7) A variable species like *P. acuminatus* is inadequately defined by descriptions of a few type specimens. The hypodigm concept (Simpson, 1940) gives a truer representation of the range of variation of the species.

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A NEW FAMILY OF CLYPEASTROID ECHINOIDS[1]

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ABSTRACT—On the basis of plate arrangement within the test, certain morphologic differences, and geographic and geologic distribution, the new family Neolaganidae, with *Neolaganum*, n. gen., as type, is proposed for New World laganoid echinoids, and the family Laganidae is emended to exclude these forms. The family Neolaganidae includes the following genera: *Neolaganum*, n. gen., type species *Laganum archerensis* Twitchell; *Cubanaster* Sanchez Roig, 1952, type species *Jacksonaster torrei* Lambert; *Neorumphia*, n. gen., type species *Rumphia elegans* Sanchez Roig; *Sanchezella*, n. gen., type species *Jacksonaster sanchezi* Lambert; *Weisbordella*, n. gen., type species *Peronella caribbeana* Weisbord; and *Wythella*, n. gen., type species *Laganum eldridgei* Twitchell. It is considered probable that many, if not all, of the New World species which have been referred to *Sismondia* Desor should be referred to the new family. All New World species, excepting possibly *Jacksonaster chilensis* Lambert and Thiéry, which have been referred to the genera *Laganum*, *Peronella*, *Rumphia*, and *Jacksonaster* are to be referred to the Neolaganidae. *Jacksonaster chilensis*, from the Pliocene of Chile, cannot be properly evaluated on the basis of the figures.

INTRODUCTION

WITHIN the Lower Tertiary of the Gulf of Mexico-Caribbean area, a group of flattened "sand dollar"-like echinoids, very similar in appearance to members of the Indo-Pacific genera *Laganum* Linck, *Jacksonaster* Lambert and Thiéry, *Peronella* Gray, and *Rumphia* Desor, occur, sometimes in considerable profusion. The species of this New World group, because of their external morphology have all, until recently (Sanchez Roig, 1952) been referred to the genera listed above, the type species of which are all living in the Indo-Pacific.

Recently, comprehensive studies of the test of clypeastroid echinoids have shown that the plate arrangement, particularly on the oral surface, is highly significant in classification and in indicating relationships of echinoids of this general type. Studies of the type species, and others, of the Indo-Pacific laganid genera show that they form a well defined group characterized by certain structural and morphologic features, and geographic as well as temporal unity. Similarly the Gulf of Mexico-Caribbean echinoids commonly referred to the various laganid genera are characterized by structural and morphologic features different from those of the Indo-Pacific as well as by having a different geologic range. The unity of each group plus the fact that each is composed of a number of distinct genera make it apparent that each should be regarded as of family rank. In the case of the neotropical group several new genera are needed in which to place the species formerly assigned to the Indo-Pacific genera. From the current studies it is apparent that within the "sand dollar"-like echinoids there is a great deal of homeomorphy, presumably due, in part at least, to convergence because of a similar mode of life. Much of this homeomorphy can only be detected by a study of the plate arrangement within the test although many small features, previously considered to be without great significance in classification are associated with the structural differences.

Particular thanks are due Dr. Mario Sanchez Roig of Havana, Cuba, for his kindness in supplying specimens of the commoner Cuban species and loaning from his own collection examples of some of the rarer species.

Note: In the figure explanations the abbreviation UCMP = University of California, Museum of Paleontology.

SYSTEMATICS

The classification of laganoid echinoids here proposed is as follows:

Family LAGANIDAE Desor, emended

Laganidae DESOR, 1857, Synopsis Echin. Fossiles, p. 217.

[1] A contribution from the Museum of Paleontology of the University of California.

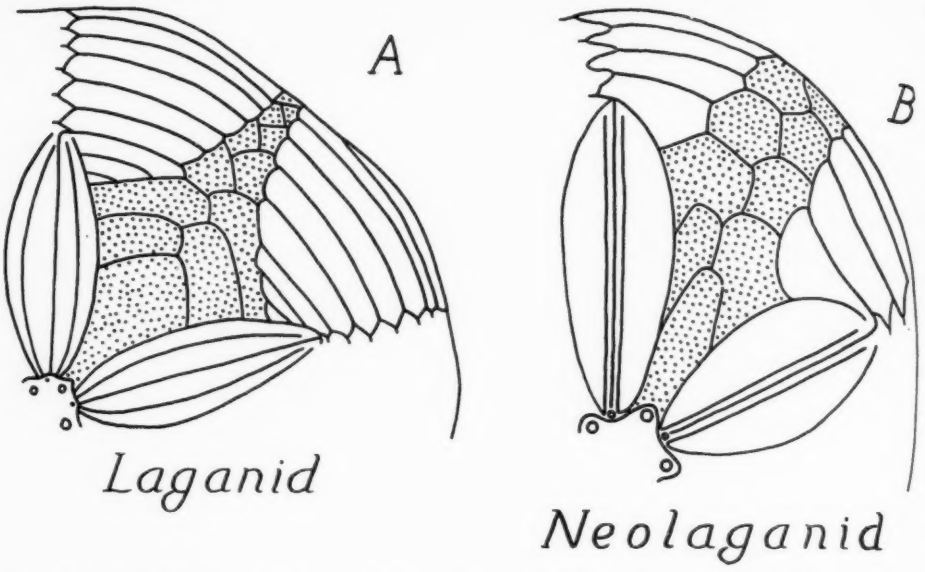

FIG. 1—Adapical right anterior interambulacra (interambulacrum 2, stippled) of characteristic genera. A. Laganid, *Laganum laganum* (Leske), ×2, hypotype, UCMP 33258, a typical laganid. B. Neolaganid, *Sanchezella sanchezi* (Lambert), ×3, hypotype, UCMP 33260, a typical neolaganid.

Test flattened, internal radial and concentric supports; ambulacra distinctly petaloid aborally, plates all primaries, outer member of pore-pair slightly elongated; interambulacra very narrow, terminated adapically by a single plate only (fig. 1A); oral surface usually with simple ambulacral food grooves not reaching margin; basicoronal plates in a pentameral star (fig. 2E-F) with ambulacral plates forming apices; basicoronal ambulacral plates larger and longer than interambulacral plates; no marked size differentiation in oral post-basicoronal ambulacral plates; periproct on oral surface; no spicules in tubefeet or internal organs; aboral miliary spines terminating in a crown.

Typical genus: *Laganum* Linck, 1807 (fig. 2E).

Other genera to be referred to the family are: *Hupea* Pomel, 1883, *Jacksonaster* Lambert and Thiéry, 1914, *Peronella* Gray, 1855 (fig. 2F), *Peronellites* Hayasaka and Morishita, 1947, *Rumphia* Desor, 1857, and *Sismondia* Desor, 1857. The last named genus is usually placed with the fibulariids but structurally it is close to *Laganum*.

Most of the New World species referred to the above named genera can be readily shown to belong to the family Neolaganidae discussed below, but a few of them (perhaps because no specimens have been available for examination) require special consideration. *Jacksonaster chilensis* Lambert and Thiéry (1909–1925 [1914], p. 313, pl. 8, figs. 5–7) from the "Pliocene" of Chile is one of these. The ambulacral food grooves are suggestive of a laganoid echinoid but the general shape is more characteristic of species of *Clypeaster* such as *C. ravenelii* (Agassiz), which also has indistinct ambulacral food grooves. Unfortunately the details of the figure are not adequate to indicate whether this is a *Clypeaster* or a laganid. If it is a laganid s.s. it could be a trans-Pacific migrant which did not become permanently established. It is also possible that the species is a neolaganid and that its age is incorrectly determined (all other neolaganids are of Eocene-Oligocene age) but the marked pentogonal outline with the interambulacral margins indented is not like that of any other neolaganid.

The New World species which have been referred to *Sismondia* require even more careful consideration. Unfortunately no specimen representing any of them has been available for examination. The following

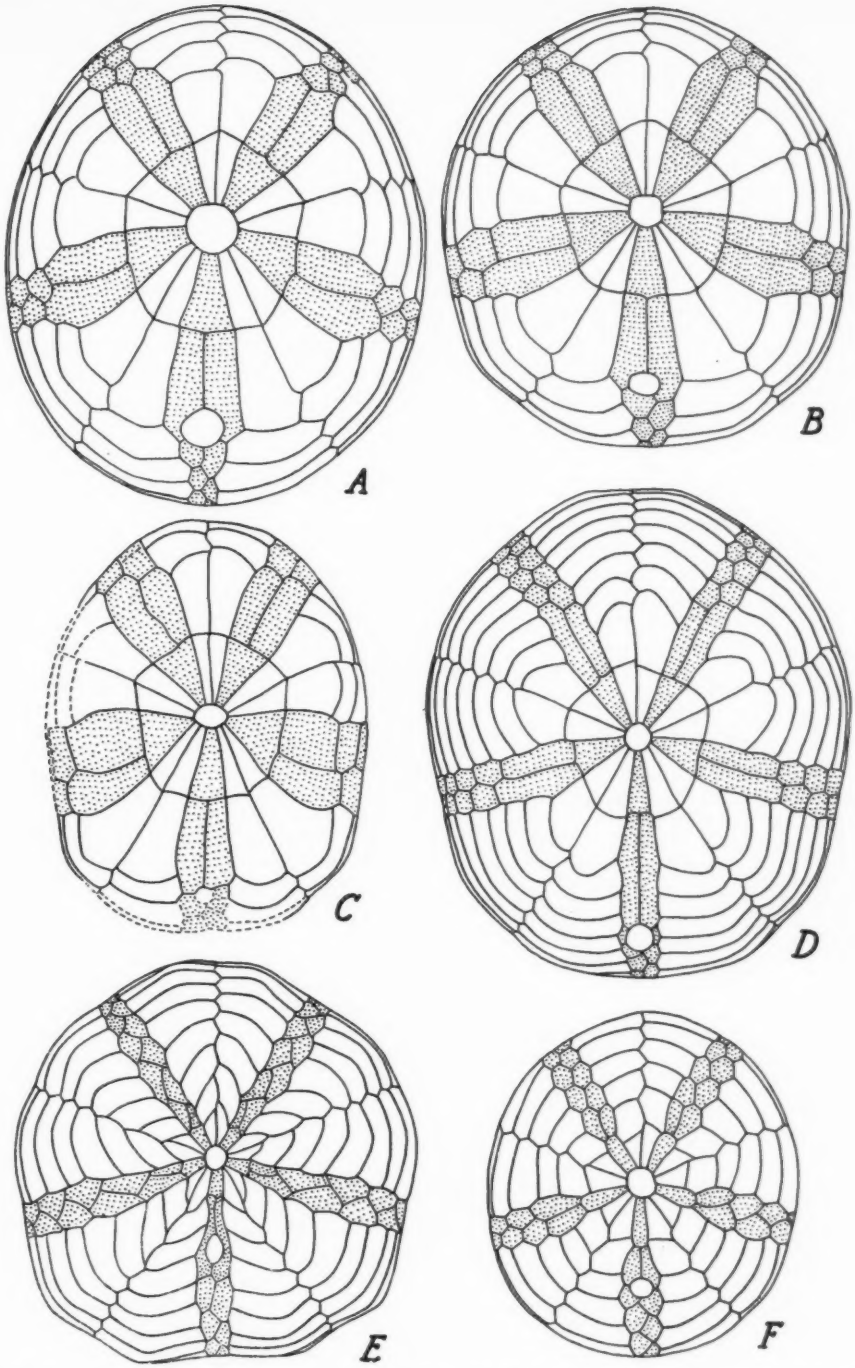

FIG. 2—Oral surface (interambulacra stippled) of laganid (E–F) and neolaganid (A–D) type species. A. *Weisbordella caribbeana* (Weisbord) ×2, hypotype, Sanchez Roig coll. B. *Neolaganum archerensis* (Twitchell), ×2.4, hypotype, UCMP 33296. C. *Neorumphia elegans* (Sanchez Roig), ×0.7, hypotype Sanchez Roig coll. D. *Cubanaster torrei* (Lambert), ×1.8, hypotype, UCMP 33297. E. *Laganum laganum* (Leske), ×0.9, hypotype, UCMP 33259. F. *Peronella peronii* (Agassiz), ×1.7, hypotype, Mus. Comp. Zool. loc. 2265.

species have been referred to *Sismondia* at one time or another: *Sismondia alta* Conrad, 1865, now considered a synonym of *Periarchus lyelli* (Conrad); *Sismondia marginalis* Conrad, 1865, now considered a synonym of *Protoscutella conradi* (Cotteau); *Sismondia plana* Conrad, 1865, now referred to *Protoscutella; Scutella crustuloides* Morton, here referred to the Neolaganidae; *Sismondia occitana* Defrance (Sanchez Roig, 1949, p. 65); *S.* aff. *S. crustula* Clark [Hawkins] (Sanchez Roig, 1949, p. 65); *S. antillarum* Cotteau (Cotteau 1875; Jackson, 1925, p. 30, pl. 2, figs. 6, 7); *S. anguillae* Cotteau (Cotteau 1875; Jackson, 1922, pp. 30–31, pl. 2, figs. 8–9); and *S. crustula* Hawkins (1927, pp. 78–79, pl. 22, figs. 4–5). The details of the figures and of the descriptions of *S. occitana* of Sanchez Roig, *S.* aff. *S. crustula* of Sanchez Roig, *S. antillarum* Cotteau, and *S. anguillae* Cotteau are inadequate to allow any conclusions as to the correctness of the generic reference. One figure (Hawkins, 1927, pl. 22, fig. 4) of *S. crustula* Hawkins indicates that there are two rows of large primary tubercles inside the petals of this species, in a manner comparable to that in *Cubanaster torrei* (Lambert). These large primary tubercles indicate the presence of compound plates in the petals in the laganoid echinoids and consequently would point to this species being a neolaganid and not referable to *Sismondia*. According to Hawkins *S. antillarum* Cotteau is very similar to *S. crustula*, consequently it would seem probable that it is a neolaganid also. In view of this it seems best at present to consider that there are no New World species which can be unequivocably assigned to *Sismondia* and that some, at least, are referable to the family Neolaganidae.

Family NEOLAGANIDAE Durham, n. fam.

Test flattened, internal radial and concentric supports; petaloid area often with compound plates (fig. 3A-C); ambulacra distinctly petaloid aborally, outer pore of porepairs greatly elongated; interambulacra very narrow, terminated adapically by a single plate only (fig. 1B); oral surface with simple ambulacral food grooves not reaching margin; basicoronal plates in a regular pentagon (figs. 2A-D, 3D-E) with ambulacral plates at apices; first post-basicoronal ambulacral plates larger than later plates on oral surface; periproct on oral surface; presence or absence of spicules in internal organs and tubefeet unknown; character of aboral miliary spines unknown.

Typical genus: *Neolaganum*, n. gen., (type species, *Laganum archerensis* Twitchell). *Cubanaster* Sanchez Roig, 1952, is the only previously described genus referable to the family.

The diagnoses of genera referable to the family are as follows:

Genus NEOLAGANUM Durham, n. gen.

Type species: *Laganum archerensis* Twitchell (fig. 2B).

Small to moderate sized, slightly pentagonal, flattened "laganid" echinoids; oral surface flat, apical area slightly raised, upper surface of test very slightly depressed inside margin at end of petals; petals elongate, slightly raised, almost closed, length two-thirds radius of test; pore-pairs conjugate, outer pore elongate; plates within petals compound, composed of dyads and triads; apical system slightly anterior; four genital pores with two posterior pores more distally situated than two anterior pores; hydropores in a branching groove as in *Laganum*; periproct on oral surface, about one-fourth distance from margin; peristome small, slightly anterior; simple ambulacral food grooves, extending about half way to margin; basicoronal plates large, forming a pentagon around peristome, ambulacral plates about one-half as wide as adjacent interambulacral plates; first pair of post-basicoronal interambulacral plates elongated, extending nearly to ambitus, two to three small additional plates between them and ambitus.

This genus is characterized by the moderate number of plates on the oral surface and the groove on the madreporite into which the hydropores open. This groove, the more pentagonal shape, especially posteriorly, and the flat or nearly flat oral surface distinguish this genus from *Weisbordella*, n. gen.

The presence of the groove in the madreporite in the laganoid echinoids has had but little attention, yet according to the present studies it is widely present and significant, being characteristic of *Laganum* but not present in *Peronella* for instance. It seems to

be widely present in the Neolaganids, although there are a number of species that have not been examined. The available data would seem to indicate that it is at least of generic importance. For instance, on other grounds (flatness of oral surface) Cooke (1942) referred *Laganum archerensis* (with groove) to *Rumphia* Desor and *Peronella caribbeana* (without groove) to *Peronella* Gray. In the present studies the groove in the madreporite seems to be a more significant difference. If these differences should be found to be of lesser value, *Neolaganum* should have priority over *Weisbordella*.

The type species is from the upper Eocene of the Gulf Coast.

Genus CUBANASTER Sanchez Roig

Cubanaster Sanchez Roig, 1949, Paleont. Cubana, vol. 1, p. 105 (nomen nudum)
Cubanaster Sanchez Roig, 1952, Torreia, no. 16, p. 3.

Type species: *Jacksonaster torrei* Lambert (fig. 2D), original designation.

Small to moderate sized, more or less ovate, pentagonal, flattened "laganid" echinoids; oral surface flat, aboral surface more or less depressed inside margin; petals approximately flush with surface, elongate, slightly open, length about three-fourths radius of test; pore pairs conjugate, outer pore greatly elongated; plates within petals partially compound, with some dyads; apical system slightly anterior; genital pores four; hydropores in a groove; peristome slightly anterior, rounded; periproct on oral surface, about one-sixth distance from margins; ambulacral food grooves simple, extending out about one-half distance to margin; basicoronal plates large, ambulacrals about equivalent to interambulacrals; first pair of post-basicoronal interambulacral plates elongated, extending out about half or more of the post-basicoronal distance on the oral surface, remaining interambulacral plates small; interambulacral areas narrow, about one-fourth width of adjacent ambulacral areas; center of periproct situated at junction of sutures between second and third post-basicoronal plates, but large in comparison to adjacent plates, so that it also comes in contact with first and fourth pair of plates.

This genus is easily separable from the other neolaganids by the large number of plates on the oral surface, the narrow interambulacra on the oral surface, and the elongate petals flush with the aboral surface.

In addition to the type species, *Jacksonaster acunai* Lambert, *J. santanae* Sanchez Roig, *J. depressus* Sanchez Roig, *Cubanaster camagüeyensis* Sanchez Roig, *C. herrerai* Sanchez Roig, *C. sandiegensis* Sanchez Roig, *C. planipetalum* Sanchez Roig, *C. santanae* Sanchez Roig, and perhaps *J. cubensis* Lambert, *J. remediensis* Sanchez Roig, and *J. sandiegensis* Sanchez Roig, are to be referred to this genus. It is known from the upper Eocene of the West Indies and Panama.

Genus NEORUMPHIA Durham, n. gen.

Type species: *Rumphia elegans* Sanchez Roig (figs. 2C, 3C).

Rather large, elongate, posteriorly truncated, "laganid" echinoids; oral surface slightly concave, aboral surface raised centrally; margins of test moderately thick; petals fairly long, length about three-fourths radius of test, usually slightly pointed, almost closed; petals with plates compound, mostly triads and tetrads; pore-pairs conjugate, outer pore elongate, pore-pair approximately normal to axis of petal; genital pores four, just inside re-entrants between petals; hydropores apparently in a branching groove; peristome slightly anterior, compressed in an anterior-posterior direction; periproct rounded, large, distant about twice its diameter from margin; basicoronal plates large, all about same length, interambulacral plates about twice as wide as adjacent ambulacrals; first post-basicoronal interambulacral plates considerably elongated, remaining interambulacral plates on oral surface small; interambulacral areas, except 5, about half as wide as ambulacral areas at ambitus, interambulacrum 5 very narrow at ambitus; periproct between second pair of post-basicoronal interambulacral plates.

Laganum lamberti Sanchez Roig and *L. santanae* Sanchez Roig, from the upper Oligocene of Cuba, are other species which appear to be referable to this genus. The compound plates within the petals of *L. lamberti* are mostly triads. The plates in the petals

of the other species have not been examined. Contrary to Sanchez Roig's description, the type specimen of his *Laganum lamberti* has only four genital pores. Similarly a specimen of his *L. santanae*, lent by him for examination, also has only four genital pores.

The available data would seem to indicate that the genus is restricted to the upper Oligocene.

The few plates on the oral surface combined with the elongate oval shape and petals flush with surface are characteristic of the genus.

Genus SANCHEZELLA Durham, n. gen.

Type species: *Jacksonaster sanchezi* Lambert (figs. 1B, 3B, 3E).

Moderate sized, elongate, thickened, "laganid" echinoids; oral surface moderately concave; margins of test thick, rounded; oral surface of test slightly arched in anterior-posterior direction; upper surface slightly concave; petals depressed, elongate, open; pore-pairs conjugate, outer pore elongate; petals with occasional dyad plates; apical system slightly anterior, genital pores four; hydropores in a groove; peristome slightly anterior, rounded; periproct large, rounded, on oral surface with center about one-fourth distance from margin; basicoronal plates large, mostly even, but shorter laterally than in anterior-posterior direction; first pair of post-basicoronal interambulacral plates elongated, remaining interambulacral plates on oral surface small; interambulacral areas narrow, less than one-fourth width of adjacent ambulacral areas on oral surface but widening rapidly at the ambitus; center of periproct situated at junction of sutures between second and third post-basicoronal plates, large as in *Cubanaster*.

Genus WEISBORDELLA Durham, n. gen.

Type species: *Peronella caribbeana* Weisbord (figs. 2A, 3A).

Moderate sized, slightly ovate, "laganid" echinoids; oral surface slightly concave, petaloid area raised, margin of test moderately thin; petals short, broad at base, moderately pointed but slightly open; plates within petals compound, mostly triads, but some dyads; pore-pairs conjugate, outer pore elongate, strongly inclined peripherally from axis of petal; apical system slightly anterior; genital pores four, inside re-entrants between petals; hydropores not in a groove; peristome slightly anterior, rounded; periproct large, rounded, on oral surface, distant its diameter from margin; basicoronal plates large, all about same length but interambulacral plates nearly twice as wide as adjacent ambulacral plates; first pair of post-basicoronal interambulacral plates elongated, remaining interambulacral plates on oral surface small; interambulacral areas narrow, less than one-fourth width of ambulacral areas at ambitus; periproct situated at suture between first and second pair of post-basicoronal plates.

Superficially this genus is very similar to the Indo-Pacific *Peronella* in general shape and in outline of petals. It is also similar to *Neolaganum* but does not have the groove for the hydropores which is present in that genus. According to Cooke (1942, p. 25) *Peronella quinquenodulata* Weisbord and *P. caribbeana* Weisbord are synonyms of *P. cubae* Weisbord. *Laganum dalli* Twitchell and *Peronella mirabilis* Jackson, are other species probably belonging to this genus. All are from the upper Eocene.

Genus *Wythella* Durham, n. gen.

Type species: *Laganum eldridgei* Twitchell (fig. 3D).

Moderate to large sized, more or less pentagonal, flattened "laganid" echinoids; oral surface flat; aboral surface slightly depressed inside margin, moderately raised in center; petals raised adjacent to apical system, length about two-thirds corresponding radius, distinctly petaloid in shape, closed; plates in petals compound, in triads and dyads; pore pairs conjugate, outer pore greatly elongated; apical system approximately central; genital pores four; hydropores in a groove; peristome central, rounded; periproct on oral surface, about one-fourth distance from margin; ambulacral food grooves simple and distinct for about one-half radius of test; basicoronal plates large, ambulacrals about equal to interambulacrals; first pair of post-basicoronal ambulacral and interambulacral plates moderately elongated, length about one-third the corresponding radius, later plates suc-

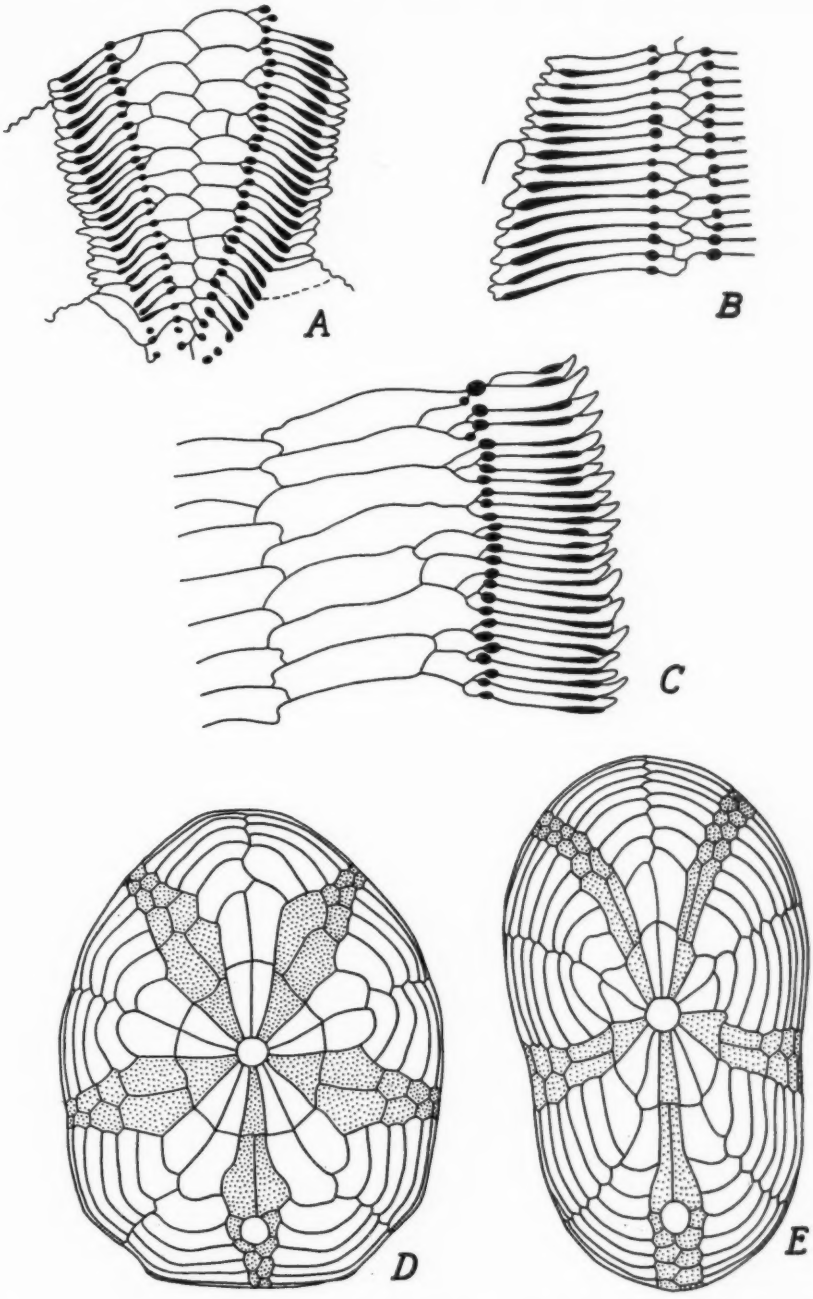

FIG. 3—Oral surface and detail of petals of neolaganid type species. A. *Weisbordella caribbeana* (Weisbord), ×7.5, outer part of left anterior petal, hypotype, Sanchez Roig coll. B. *Sanchezella sanchezi* (Lambert), ×9, medial part of right posterior petal, hypotype, UCMP 33260. C. *Neuorumphia elegans* (Sanchez Roig), ×6, medial part of right posterior petal, hypotype, Sanchez Roig coll. D. *Wythella eldridgei* (Twitchell), ×1.3, hypotype, UCMP 33261. E. *Sanchezella sanchezi* (Lambert), ×1.5, slightly restored after hypotype, UCMP 33298.

cessively smaller in altitude; interambulacral areas widen to a maximum equal to adjacent ambulacral areas at a point slightly over one-half the radius from the peristome, then narrow to the ambitus where they are about one-eighth width of adjacent ambulacra; center of periproct situated about at junction between second and third pairs of post-basicoronal plates, large in comparison to size of plates.

This genus is similar to *Cubanaster* Sanchez Roig but differs from it by the thinner margins, raised petals and wide interambulacral areas about midway on the oral surface. It also resembles *Neorumphia*, n. gen., but has far fewer plates on the oral surface, a thinner margin and narrower interambulacral areas at the ambitus.

The type is the only species now known to be referable to the genus. It occurs in the Ocala limestone, late upper Eocene of the Gulf Coast of the United States.

Specimens of several Caribbean-Gulf of Mexico "laganid" species have not been examined, but from the figures and descriptions appear to be members of this family. Until they have been carefully examined, they are left generically unassigned. These species are: *Laganum floridanum* Twitchell, *L. ocalanum* Cooke, *Scutella crustuloides* Morton, *Laganum johnsoni* Twitchell, *L. dalli* Twitchell, *L. elongatum* Egozcue, *Peronella mirabilis* Jackson, and *Laganum cubanum* Weisbord.

The New World family Neolaganidae may be readily separated from the Laganidae emended by the following characters: usually compound plates in petals; basicoronal plates arranged in a more or less regular pentagon, not in a pentagonal star; first pair of post-basicoronal plates considerably larger than following plates as contrasted to plates gradually decreasing in altitude; outer member of pore-pairs greatly elongated as contrasted to only slightly elongated; terminal adapical interambulacral plate approximately rectangular (fig. 1B) in shape as contrasted to rhomboidal (fig. 1A); range Eocene to Oligocene as contrasted to Eocene to Recent (with major expansion in Miocene to Recent); restricted to New World as contrasted to Old World and Indo-Pacific.

It is to be noted that the large primary tubercles within the petals of many of the Neolaganidae are indicative of the compound nature of the plates. Insofar as the author is aware these large tubercles are not found in any of the Laganidae proper as here restricted.

MANUSCRIPT RECEIVED NOVEMBER 30, 1953

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THE CLASSIFICATION OF THE PALEOZOIC AMMONOIDS

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ABSTRACT—An outline classification is presented, in which the Paleozoic ammonoids are placed in 35 families, grouped into 14 superfamilies and 5 suborders. Each of these is discussed briefly. New names are proposed for two genera (*Delépinoceras* and *Uddenoceras*) and three suborders (Bactritina, Anarcestina, and Prolecanitina).

THIS paper is the fourth and last in a series of studies on the classification of the Ammonoidea, prepared in conjunction with work on the *Treatise on Invertebrate Paleontology*. The other three have dealt with the Triassic, Jurassic, and Cretaceous forms and they have all been published in this Journal (Kummel, 1952; Arkell, 1950; and Wright, 1952). Acknowledgment is due to Professors Bernard Kummel and O. H. Schindewolf for advice in regard to certain of the familial names.

The origin of the ammonoids has remained a moot question. It was long ago suggested by Sandberger that *Bactrites*, which has a straight conch, is an ammonoid. Hyatt then postulated that the typical ammonoids evolved from *Bactrites* through the loosely coiled *Gyroceratites* [= *Mimoceras*] and the more tightly coiled *Anarcestes*, in which, however, the umbilicus is perforate. More recently Spath (1933) challenged this view and concluded that the ammonoids most probably evolved from some coiled Silurian nautiloids of the general type of *Barrandeoceras*. Schindewolf has supported Hyatt's view and has emphasized that in some species of *Anarcestes*, the extreme adapical part of the conch is essentially straight and then loosely coiled (fig. 1). Spath has countered with the argument that it is not significant that "Devonian goniatites at first had imperfectly closed umbilici, [as] this is only what would be expected in forms still so near to the ancestral nautilicones."

One of the chief deterrents to the Hyatt hypothesis was the fact that several genera of coiled ammonoids were known from the Lower Devonian, whereas *Bactrites* had not been found to occur below the Middle Devonian. *Eobactrites* of the Ordovician of Bohemia is most probably not the progenitor of *Bactrites* because no intermediate forms are known from the Silurian. However, Erben has recently recorded the discovery of *Lobobactrites* in the Lower Devonian of Germany. This genus, which has slightly sinuous sutures, is regarded by Schindewolf as a descendant of *Bactrites* (with which it is more or less gradational) whereas Spath believed that both it and *Gyroceratites* "are derivatives of goniatites."

All of these conclusions seem to be equivocal. However, it should perhaps be stated that the oldest undoubted ammonoids, which are from the Lower Devonian, are reminiscent of certain contemporaneous and slightly older coiled nautiloids. Nevertheless, the thin-walled gradually expanded conch, the bulbous calcareous protoconch, the slightly sinuous sutures, and the small marginal orthochoanitic siphuncle of the bactritids are suggestive of the early ammonoids. Even if the bactritids are the ancestors of the coiled ammonoids, their taxonomic position remains in question, for they can be assigned with about equal propriety to either order of the Tetrabranchiata. Ac-

FIG. 1—Adapical portion of a Lower Devonian ammonoid, *Anarcestes simulans* (Barrande) of Bohemia, showing a slightly curved protoconch, a loosely coiled first half-volution of the conch, and a large umbilical perforation, about ×17. After Schindewolf.

cordingly, we have not included them on the accompanying phylogenetic chart, though they are listed with question in our outline classification.

Modern paleontological investigations have led to a considerably different understanding of the phylogeny and therefore the classification of the Paleozoic ammonoids than appeared in the classical literature of the turn of the century. Many of the data have been published in both Europe and this country, especially by Schindewolf, Schmidt, Spath, Ruzhencev, Delépine, Basse, Plummer, Scott, and ourselves. In 1925 Schmidt and in 1934 Spath issued phylogenetic charts which ably summarized the present philosophy, as we understand it. That of the latter author anticipates the major features of ours. We have been concerned with this general subject over a period of time as is evidenced by the classification of Devonian forms published in 1937, that of Permian in 1940, and that of Carboniferous included in a still unpublished manuscript completed and submitted early in 1940 for inclusion in a general report on the Late Paleozoic of the North American Mid-Continent region.

After careful consideration, we have decided to divide the Paleozoic ammonoids (exclusive of the Bactritina) into 35 families and to group these into 14 superfamilies, which are placed in 5 suborders. One of the suborders (the Ceratitina) includes all of the superfamilies known from the Triassic except the Medlicottiaceae and the Phylloceratoceae. The former of these is represented in the Triassic by only a very few genera, and it became extinct during that period. The latter, the Phylloceratoceae, is the stock which is generally believed to have been ancestral to all post-Triassic ammonoids.

We have attempted to base superfamilies chiefly on fundamental differences in the sutures, and to put them on a par with one another, as well as with those of the Mesozoic. It should be kept in mind that practically all of the Triassic ammonoids to have evolved from a single stock of Paleozoic forms, and that, similarly, all of the Jurassic ammonoids came from one Triassic group. Because of these beliefs and because the Triassic and the Jurassic are thought to be of relatively short duration, the basic diversity of ammonoids during those periods might be expected to be less than that of the Cretaceous and especially the Paleozoic.

The classifications proposed by previous authors have emphasized such characters as the shape of the conch, the length of the body chamber, the position of the siphuncle, and the "ornamentation" of the test, as well as the configuration of the sutures. We are of the opinion that all of these features are important in ammonoid taxonomy, but that, at least in the Paleozoic forms, the one listed last is perhaps the best guide to the phylogenetic relationships. As a matter of fact, the generic affinities of most Paleozoic ammonoids can be determined from the shape of the sutures alone, a character in which homeomorphy is relatively rare and easily recognized. Furthermore, the ontogenetic development of the sutures is a general guide to the phylogeny of the group though, to be sure, the early stages of some forms do not resemble in detail the mature sutures of their progenitors. The fossil record of the Paleozoic ammonoids is perhaps now well enough known to permit us to make certain general assumptions and to deny others. Accordingly, we have attempted to take all factors into account and to prepare a general classification of the Paleozoic ammonoids.

Familial names used in the proposed classification are in accordance with the *Copenhagen decisions on zoological nomenclature* (Hemming et al., 1953). In each case we have given in square brackets the original name. No consideration has been given to such subjective matters as the original authors' interpretations of scope. We have regarded all familial names as coordinate and have ignored informal names. Furthermore, we have interpreted as superfamilies, taxonomic groups composed of families, unless it is clear that they were intended to be suborders or units of a higher category. We have, of course, attempted to locate original authors, but experience has convinced us that almost certainly there are cases in which we have overlooked the first usage. We will appreciate having any lapses called to our attention so that in the forthcoming *Treatise* the names can be properly ascribed. The ending of the superfamily names is that

employed by Arkell, Wright, and Kummel in the papers cited.

Class CEPHALOPODA Leach, 1817
[les céphalopodes Cuvier, 1797]

Subclass TETRABRANCHIATA Owen, 1832

Order AMMONOIDEA Zittel, 1884

Suborder BACTRITINA Miller & Furnish, n. suborder [Nautiloidea?]

Superfamily *Bactritaceae*
Family Bactritidae Hyatt, 1884

Suborder ANARCESTINA Miller & Furnish, n. suborder

Superfamily *Anarcestaceae*
Family Mimoceratidae [Mimoceratinae] Steinmann, 1890
Family Agoniatitidae Holzapfel, 1899
Family Anarcestidae [Anarcestinae] Steinmann, 1890
Superfamily *Prolobitaceae*
Family Prolobitidae Wedekind, 1913
Superfamily *Gephuroceratacеae*
Family Gephuroceratidae [Gephyroceratidae] Frech, 1901
Family Beloceratidae [Beloceratinae] Frech, 1902

Suborder CLYMENIINA [CLYMENINAE] Hyatt, 1884

Superfamily *Gonioclymeniaceae*
Family Hexaclymeniidae Lange, 1929
Family Gonioclymeniidae [Gonioclymenidae] Hyatt, 1884
Family Miroclymeniidae [Miroclymeninae] Schindewolf, 1924*
Family Glatziellidae [Glatziellinae] Schindewolf, 1928
Superfamily *Clymeniaceae*
Family Clymeniidae [Clymenidae] Edwards, 1849
Family Parawocklumeriidae [Parawocklumeridae] Schindewolf, 1937
Family Platyclymeniidae Wedekind, 1914
Family Rectoclymeniidae Schindewolf, 1923

Suborder GONIATITINA [GONIATITINAE] Hyatt, 1884

Superfamily *Cheiloceratacеae*
Family Tornoceratidae [Tornoceratea] Arthaber, 1911
Family Cheiloceratidae Frech, 1897
Superfamily *Agathiceratacеae*
Family Agathiceratidae Arthaber, 1911
Family Shumarditidae Plummer & Scott, 1937
Family Perrinitidae Miller & Furnish, 1940
Superfamily *Cyclolobaceae*
Family Popanoceratidae Hyatt, 1900
Family Cyclolobidae Zittel, 1895
Superfamily *Goniatitaceae*
Family Goniatitidae [Goniatitea] de Haan, 1825
Family Neoicoceratidae Hyatt, 1900 [=Gastrioceratea Arthaber, 1911]
Family Metalegoceratidae Plummer & Scott, 1937
Family Schistoceratidae Schmidt, 1929
Superfamily *Adrianitaceae*
Family Adrianitidae Schindewolf, 1931
Superfamily *Dimorphoceratacеae*
Family Dimorphoceratidae [Dimorphoceraе] Hyatt, 1884
Family Thalassoceratidae Hyatt, 1900

Suborder PROLECANITINA Miller & Furnish n. suborder

Superfamily *Prolecanitaceae*
Family Prolecanitidae Hyatt, 1884
Family Prodromitidae Arthaber, 1911
Family Daraelitidae [Daraelitinae] Tchernow, 1907
Superfamily *Medlicottiaceae*
Family Pronoritidae [Pronoritinae] Frech, 1901
Family Medlicottiidae [Medlicottinae] Karpinsky, 1889
Family Sageceratidae Hyatt, 1900 [Triassic]

Suborder CERATITINA [CERATITINAE] Hyatt, 1884

Superfamily *Otoceratacеae*
Family Paraceltitidae Spath, 1930
Family Xenodiscidae [Xenodiscinae] Frech, 1902
Family Otoceratidae Hyatt, 1900 [Triassic]
Family Ophiceratidae [Ophiceratinae] Arthaber, 1911 [Triassic]
Family Dieneroceratidae Kummel, 1953 [Triassic]

* Schindewolf (March 16, 1954) prefers for this family his 1937 name Wocklumeriidae [Wocklumeridae].

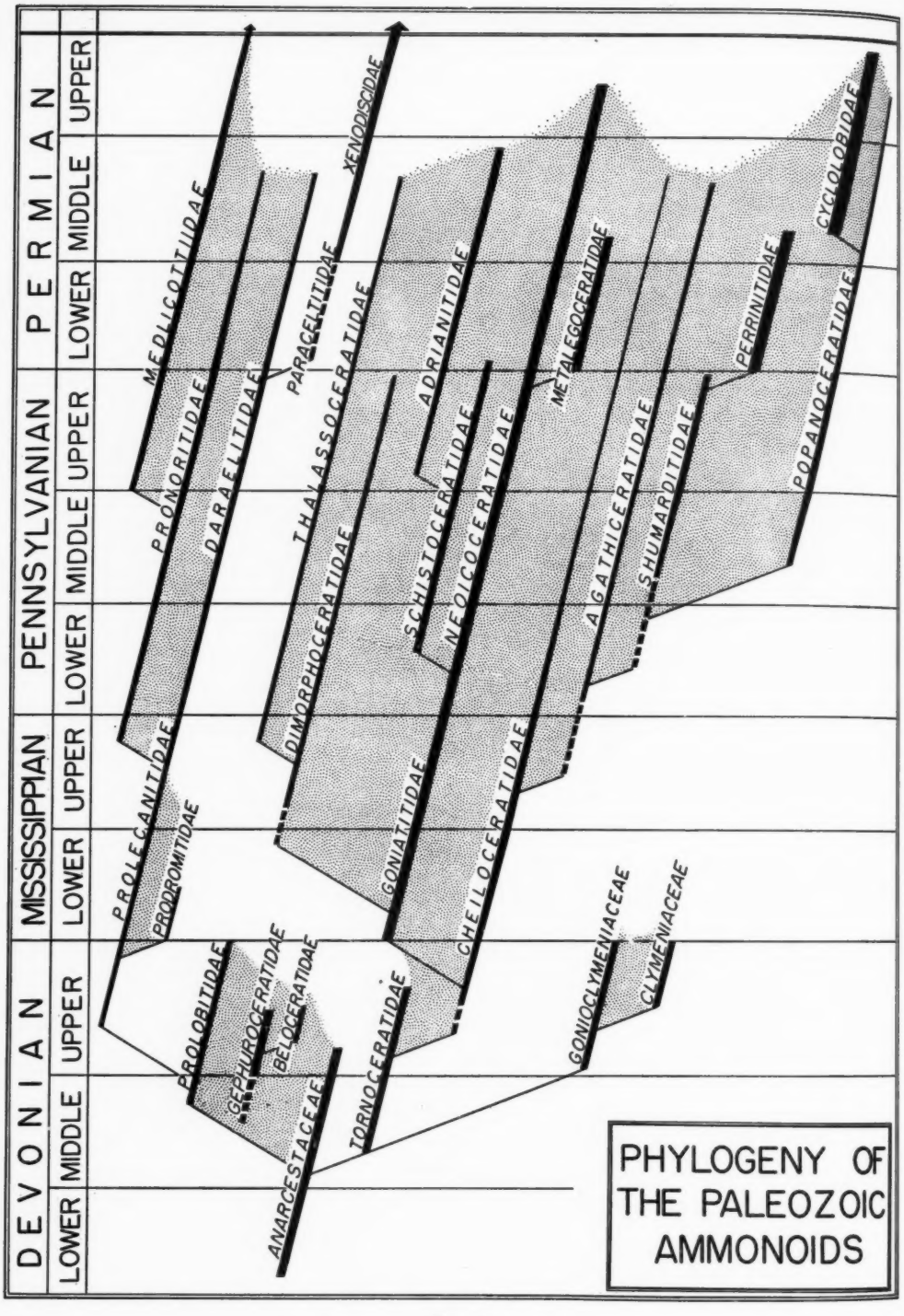
DEVONIAN
MISSISSIPPIAN
PENNSYLVANIAN
PERMIAN
LOWER
MIDDLE
UPPER
LOWER
UPPER
LOWER
MIDDLE
UPPER
LOWER
MIDDLE
UPPER
PROLECANITIDAE
PRODROMITIDAE
PROLOBITIDAE
GEPHUROCERATIDAE
BELOCERATIDAE
ANARCESTACEAE
TORNOCERATIDAE
MEDLICOTTIIDAE
PRONORITIDAE
DARAELITIDAE
PARACELTITIDAE
XENODISCIDAE
THALASSOCERATIDAE
DIMORPHOCERATIDAE
GONIATITIDAE
CHEILOCERATIDAE
ADRIANITIDAE
SCHISTOCERATIDAE
NEOICOCERATIDAE
METALEGOCERATIDAE
AGATHICERATIDAE
SHUMARDITIDAE
PERRINITIDAE
CYCLOLOBIDAE
POPANOCERATIDAE
GONIOCLYMENIACEAE
CLYMENIACEAE
PHYLOGENY OF THE PALEOZOIC AMMONOIDS

FIG. 2

Superfamily *Noritaceae* [*Noritinae*] Karpinsky, 1889 [Triassic]
Superfamily *Ceratitaceae* [*Ceratitidae*] Mojsisovics, 1879 [Triassic]
Superfamily *Clydonitaceae* [*Clydonitidae*] Mojsisovics, 1879 [Triassic]
Superfamily *Tropitaceae* [*Tropitidae*] Mojsisovics, 1875 [Triassic]
Superfamily *Lobitaceae* [*Lobitinae*] Mojsisovics, 1882 [Triassic]
Superfamily *Arcestaceae* [*Arcestidae*] Mojsisovics, 1875 [Triassic]
Superfamily *Ptychitaceae* [*Ptychitinae*] Mojsisovics, 1882 [Triassic]
Superfamily *Pinacocerataceae* [*Pinacoceratidae*] Mojsisovics, 1879 [Triassic]

The forthcoming unit of the *Treatise* will include discussions of each of the above taxonomic units, as well as their major subdivisions. Therefore, we will here present only sufficient data to make clear the general nature of our proposed classification.

The Anarcestina, as we interpret the suborder, is the ancestral stock of the ammonoids. Its most primitive representatives are the Anarcestaceae. Forms with only slightly sinuous sutures, non-involute whorls, and perforate umbilici are placed in the Mimoceratidae. Those with simple but nevertheless rather sinuous sutures, deeply involute conchs, compressed whorls, and imperforate umbilici are assigned to the Agoniatitidae. Similar forms with low whorls and relatively broad conchs constitute the Anarcestidae. The superfamily is known to be widespread geographically, but stratigraphically it is confined to the Devonian. All the Lower Devonian representatives are from Europe.

The Prolobitaceae, which consists of only one family, is distinguished primarily by the sutures. These are characterized especially by the fact that the primary lateral lobes evolved on the flanks of the conch and remained there throughout ontogenetic development. The lobes of the sutures are few in number and are undivided. Stratigraphically the superfamily is limited to the latter half of the Devonian, and geographically it seems to be limited to the eastern hemisphere.

The Gephuroceratacеae is a small compact unit that is characteristic of the early Upper Devonian all over the world. The large prominently subdivided ventral lobe distinguishes its members from all other Devonian ammonoids but is superficially similar to that of the late Paleozoic goniatitids. The Beloceratidae evolved from the Gephuroceratidae by the addition of secondary elements to the sutures.

The Clymeniina have long been regarded as quite distinct from other ammonoids because of the dorsal position of their siphuncle. The group is quite diverse, it is limited to the Upper Devonian, and it is world-wide in its distribution. The oldest known representative, *Acanthoclymenia*, is from the early Upper Devonian of New York, but clymenioids are far rarer in the western than in the eastern hemisphere. They are generally regarded as excellent index fossils. Schindewolf has summarized the taxonomy of the suborder.

The Goniatitina constitutes the great bulk of the Paleozoic ammonoids. During the latter part of the era, its members underwent marked evolution and became quite varied. Among them are some of our best index fossils. The basic suture of the group consists of four pairs of lobes, though certain of the primitive representatives in the Cheiloceratacеae did not attain that stage. The suborder is divided into superfamilies primarily on the basis of major modifications of the basic elements of the sutures.

The Cheiloceratacеae, as interpreted by us, consists of two families, the Tornoceratidae and the Cheiloceratidae. In both of these the sutures typically consist of three pairs of lobes of which the external lateral pair arises adventitiously. According to Wedekind (1918, pp. 103, 134, 141) the chief difference between the two families lies in the fact that in the Tornoceratidae the growth lines are biconvex, whereas in the Cheiloceratidae they are convex. Members of the former family are widespread and locally abundant in the Middle and Upper Devonian, whereas cheiloceratids appear in the Upper Devonian, are abundant in the early Mississippian, and continue into the Middle Permian. This latter family is the stock that gave rise to the rest of the Goniatitina.

The Agathicerataceae contains forms in which the three pairs of external lateral lobes originated as subdivisions of a single pair of goniatitid lateral lobes. The super-

family made its debut in the early Pennsylvanian, became fairly abundant during the latter part of the same period, and climaxed in the Permian. The Agathiceratidae, the most primitive family of the group, is a long-ranging stable unit. The Shumarditidae is quite variable in both form and occurrence. The Perrinitidae, a closely knit group confined to the first half of the Permian, has the same number of major sutural elements, which, however, are strongly digitate. Members of the last family are among the best of index fossils.

The Cyclolobaceae are characterized especially by the possession of a series of auxiliary lobes in their sutures, which generally are ceratitic. Primitive members of both the Popanoceratidae and the Cyclolobidae did not develop many auxiliaries. However, in the more advanced representatives of these families the number of such lobes increased, culminating in *Cyclolobus* of the very late Permian. The Popanoceratidae appeared during mid-Pennsylvanian time and continued to the close of the Permian, being most abundant during the late Pennsylvanian and the first half of the Permian. In general, these forms are not as good index fossils as are members of the Cyclolobidae, which represent a single phylogenetic sequence that evolved during the latter half of the Permian.

The Goniatitaceae, as we interpret it, includes *Goniatites* s. s. and its affines plus the neoicoceratids (=gastrioceratids) and their immediate descendants, the metalegoceratids, and the schistoceratids. The Goniatitidae has received careful consideration over a period of many years and the general evolutionary development is well known. Morphological details which are not believed to be particularly significant in other groups seem to have stratigraphic value in this family. The basic suture was evolved during early ontogenetic development, and then the number of lobes remained constant. Neoicoceratids are very widespread and abundant in the Pennsylvanian and the Permian, but, except in a general way, they are of limited stratigraphic value. The Metalegoceratidae, the last of the superfamily to be recognized, consists of a very few genera, which are limited to the early Permian but are widespread geographically. The schistoceratids, with one exception, illustrate the development of a single evolutionary trend, viz., the progressive increase in the complexity of the suture by the addition of lobes in the umbilical regions. The exception is *Wellerites*, in which a pair of adventitious lobes is developed as prominent subdivisions of the first lateral saddles of the external sutures, a difference of subfamily significance.

The Adrianitaceae, which consists of only one family, resembles superficially certain of the Agathiceratacеae. However, in the adrianitids the sutures, which are goniatitic, consist of elements that are added in the umbilical region. Stratigraphically the superfamily is limited to the late Pennsylvanian and the Permian, but typical forms are known from only the mid-Permian. Geographically, they are of world-wide distribution.

In the Dimorphoceratacеae the sutures are basically the same as those of the Goniatitidae, but they are more or less ceratitic. Typical representatives of the Dimorphoceratidae have sutures in which the prongs of the ventral lobe are bifid. However, in advanced forms the lateral lobes of the external sutures are also bifid, and the prongs of the ventral and the lateral lobes become more or less serrate. In the thalassoceratids the prongs of the ventral lobe and the lateral and umbilical lobes are serrate; however, in the most advanced representative of this group all of the external suture is digitate and the internal lateral lobes are bifid. *Dimorphoceras thalassoide* Delépine (Depépine and Menchikoff, 1937, pp. 83-85, pl. 5, figs. 6, 7) of the Viséan near the Moroccan-Algerian border and in the Pyrenees differs from typical representatives of both of these families in that the prongs of its ventral lobe and its lateral lobes are trifid, but it is perhaps closer to the thalassoceratids than to the dimorphoceratids. Because of its unique sutures, we regard it as the type species of a new genus for which we here propose the name *Delépinoceras*. Both of the families of the Dimorphoceratacеae are known from the Mississippian and they range well up into the Permian.

The Prolecanitina is a relatively small suborder of discoidal Paleozoic ammonoids but is especially important because it is the

stock from which all Mesozoic forms arose. Presumably the group evolved from the prolobitids during late Devonian times. With one minor exception, it continued as three stable trends through the late Paleozoic. One of these persisted into the Triassic, and another gave rise to the Ceratitina, of which the chief development was in the Triassic. Members of this suborder are of much more stratigraphic value in the Mississippian than in the later Paleozoic. Characteristically the sutures form a large number of lobes, which were added progressively in the umbilical regions. It may be significant that the siphuncle is simple and retrochoanitic, much as in the Devonian goniatites and in the most primitive members of the Goniatitina.

The Prolecanitaceae includes the simplest members of the suborder. In the Prolecanitidae the sutures are goniatitic, whereas in the Prodomitidae and the Daraelitidae the lobes are serrate. The Prodomitidae consists of one unique species which is known from only the Lower Mississippian of central United States and which can be thought of as more or less "precocious" because of its similarity to the Ceratitina. The Daraelitidae is the classical example of a small compact group which exhibits an evolutionary trend that continued throughout the late Paleozoic. Both prolecanitids and daraelitids are world-wide in their distribution.

The Medlicottiaceae is widespread and abundant in the late Paleozoic and is not particularly rare in the Triassic. However, only one genus crosses the Permo-Triassic boundary. The suture forms a number of subequal anxiliary lobes. Characteristically the first lateral lobes are modified; in the Pronoritidae they are bifid, whereas in the Medlicottiidae the changes are much more extreme. Most of the genera in this superfamily have a long range in the late Paleozoic. It has been thought that the typical medlicottiids evolved from the pronoritids through *Prouddenites*, *Uddenites*, *Propinacoceras*, and *Artinskia*. However, it seems more probable that during the late Pennsylvanian *Artinskia* arose directly from *Uddenites* and then gave rise to *Propinacoceras* in the Permian. The sutures of *Uddenites oweni* Miller and Furnish (1940, pp. 34–38, pl. 2, figs. 1–6; pl. 3, figs. 9, 10; pl. 4, figs. 1, 2) of the Upper Pennsylvanian of Texas are as much or more like those of *Propinacoceras* than those of the genotype of *Uddenites*, *U. schucherti* Böse, of the same general horizon and locality. Accordingly it now seems best to recognize that the former species represents a generic step intermediate between typical *Uddenites* and *Artinskia*, and we regard it as the type species of a new genus for which we here propose the name *Uddenoceras*.

Although the Ceratitina underwent their great development in the Triassic, they are known from strata as old as the Middle Permian. The shape of their conch, the nature of their sutures, and especially the structure of their siphuncle indicate that they arose from the Daraelitidae. The first superfamily of the suborder to appear, the Otoceratáceae, includes two closely related Permian families, the Paraceltidae and the Xenodiscidae. However except on a stratigraphic basis, in many cases it is difficult to differentiate xenodiscids from Triassic ophiceratids, though the latter are in general farther advanced. The other eight superfamilies of the Certatitina are exclusively Triassic, and accounts of them have recently been published by Spath (1934 and 1951) and Kummel (1952).

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MANUSCRIPT RECEIVED MARCH 17, 1954

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NOMENCLATURAL NOTE

GUNNELLODUS, A NEW NAME FOR *IDIACANTHUS* GUNNELL

NORMAN J. WILIMOVSKY
Natural History Museum, Stanford University, California

Almost five years ago, when beginning a review of the literature on the stomiatoid fish genus *Idiacanthus*, I encountered Frank H. Gunnell's paper on the "Conodonts and fish remains from the Cherokee, Kansas City, and Wabaunsee Groups of Missouri and Kansas" Jour. Paleontology, vol. 7, pp. 261–297, pls. 31–33). In this work (page 293) the name *Idiacanthus* is proposed for a genus of fossil sharks. However, as this generic name is preoccupied by *Idiacanthus* Peters, 1876 (Monats. Ber. Akad. Wiss. Berlin, p. 846) for a deepsea fish, Gunnell's generic name is a homonym. In addition to priority, Peters' name deserves retention on the basis of usage. Although not a common fish, the bathypelagic *Idiacanthus* Peters has been rather widely treated in both faunal and systematic monographs, whereas Gunnell's recent genus is virtually unknown.

Repeated attempts to contact Mr. Gunnell since early 1950 have failed and as a consequence I now propose *Gunnellodus* as a new generic name for *Idiacanthus* Gunnell. The type of the genus remains the same, *I. bellistriatus* Gunnell.

NOTICE ON ZOOLOGICAL NOMENCLATURE

Notice is hereby given that the possible use by the International Commission on Zoological Nomenclature of its Plenary Powers is involved in the application relating to the under-mentioned names included in Part 8 of Volume 9 of the Bulletin of Zoological Nomenclature to be published in May, 1954.

Ammonites mammillatus Schlotheim, 1813, proposed designation of a neotype for, and *Douvilleiceras* de Grossouvre, 1893 (Class Cephalopoda, Order Ammonoidea), proposed designation of a type species for (pp. 250–254) (File Z. N. (S.)631).

The present notice is given in pursuance of decisions taken by the Thirteenth International Congress of Zoology, Paris, July 1948. Any specialist who may desire to comment on the foregoing application is invited to do so in writing to the Secretary to the International Commission (Address: 28 Park Village East, Regent's Park, London, N.W.1., England) as soon as possible. Every such comment should be clearly marked with the Commission's File Number as given in the above listing.

Summarized from a notice dated
5th May, 1954, signed
Francis Hemming
Secretary to the International Commission
on Zoological Nomenclature

JOURNAL OF PALEONTOLOGY, VOL. 28, NO. 5, PP. 694–707, SEPTEMBER 1954

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NOMINATIONS FOR MEMBERSHIP

In accordance with Article 3, Chapter 1, of the By-Laws of the Paleontological Society, the Secretary submits the following nominations for membership in the Society. The list has been approved by the Council of the Society.

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NOTICE

ERMINE COWLES CASE MEMORIAL FUND

Ermine Cowles Case, distinguished vertebrate paleontologist and member of the faculty of the University of Michigan for 35 years, passed away on September 7, 1953. That his life and works may be a source of inspiration to future students, and that his memory may be perpetuated on the University campus, several of his friends and colleagues would like to see established a living memorial that will emphasize, by an annual ceremony, the scholarship, industry, and intellectual honesty that characterized his career.

To this end it is proposed to establish the Ermine Cowles Case Memorial Fund, to be raised by popular subscription. Of the suggestions made for its use to accomplish the desired purpose, the Committee believes that a memorial in recognition of outstanding scholarship would be the kind of tribute Professor Case would have appreciated and which would contribute most effectively to the intellectual life and vigor of the earth sciences. We therefore propose that the Ermine Cowles Case Memorial Fund be set up to provide annually for

(a) The Ermine Cowles Case Memorial Lecture.
(b) The Ermine Cowles Case Student Award.

Both the lecture and the award would be given in the earth sciences; other attainments being the same, preference would be given to a speaker and a student in paleontology or historical geology, the fields of Professor Case's labors. The award would be made to a graduate student at the University of Michigan for outstanding scholarship and attainment in research as evidenced by the best manuscript completed for publication. If in any year no student of the earth sciences seems to merit the award, the income for that year would revert to the fund. The award would be announced on the occasion of the annual memorial lecture.

Contributions should be made payable to the Ermine Cowles Case Memorial Fund and sent to the Director, Museum of Paleontology, University of Michigan, Ann Arbor.

The Committee
E. N. Goddard
G. M. Ehlers
L. B. Kellum, Chairman

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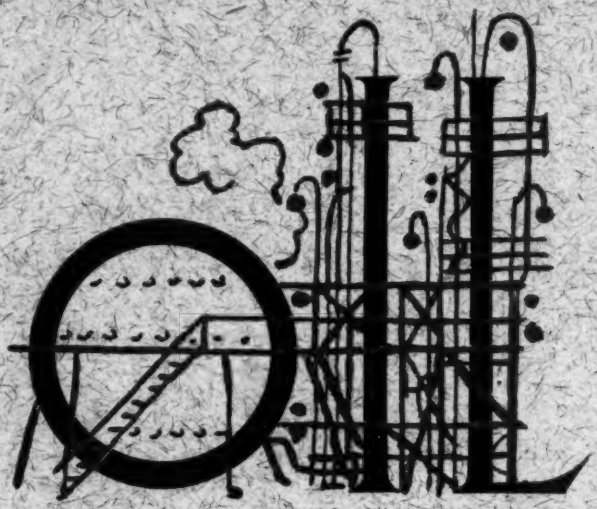

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